NESTING ECOLOGY AND INTERACTIONS BETWEEN LOCAL AND INTERNATIONAL PRIORITIES FOR HAWKSBILL SEA TURTLE (*ERETMOCHELYS IMBRICATA*) CONSERVATION ON THE PACIFIC COAST OF CENTRAL AMERICA

A Dissertation

by

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ABSTRACT

Despite human interaction with the biophysical environment since the beginning of human history, traditional research generally studied human and natural systems separately when addressing human–nature interactions. The purpose of my research is to better understand the nesting ecology and interactions between local and international priorities for hawksbill sea turtle (*Eretmochelys imbricata*) conservation in El Salvador and Nicaragua, where >90% of eastern Pacific hawksbill nesting occurs. In the first study, I explained the realities experienced by coastal residents who share habitat with hawksbills in El Salvador and then identified and clarified implications of discrepancies between these realities and international priorities for hawksbill conservation. The main findings were 1) primary importance of hawksbills is economic value attached to egg sales, but deeper cultural connections exist, 2) egg purchase by hatcheries benefits hawksbills and humans and 3) opportunities for local residents to participate in decision-making are limited and should be increased.

In the second study, I characterized the microhabitat preferences and repeatability of nest-site choice by hawksbills, and then clarified the implications of doomed egg relocation programs on gene pools of hawksbills. I found 1) hawksbills preferred nest sites with abundant vegetation on dynamic beaches in mangrove estuaries, 2) female hawksbills exhibited local adaptations to differences in nesting habitat and 3) individual hawksbills consistently placed nests under high percentages of overstory vegetation, but were inconsistent in nest placement related to woody vegetation borders.

In the third study, I generated and analyzed thermal profiles of hawksbill nest environments and estimated the sex ratios and physical condition of hatchling hawksbills under natural and artificial conditions. The primary findings were 1) minimal differences in temperature existed between sand depths, 2) adjustment of nest depth is unlikely to compensate for climate change, 3) in situ clutches incubated at higher temperatures and produced less fit offspring and 4) egg relocation can contribute to recovery efforts.

The findings of these studies offer insight into interactions between hawksbill population dynamics and local community development on the Pacific coast of Central America, and demonstrate the value of implementing an evidence-based approach to guide public policy and conservation strategies.

DEDICATION

To my incredible wife, Gabriela, and my adorable daughter, Lucia, who brought me laughter, smiles, joy, happiness, and most of all love. This, and everything I do, is for you.

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CHAPTER I

INTRODUCTION

BACKGROUND

Humans have interacted with the biophysical environment since the beginning of human history. However, traditional research generally studied human and natural systems separately when addressing human–nature interactions (Liu et al., 2007). This artificial divide can produce an incomplete or inaccurate understanding of complexly interwoven systems, which can be particularly problematic when these finding are used to guide public policy and conservation strategies for endangered species. Because the success of many policies relies on their ability to account for these complexities, there is growing concern that existing policies and associated conservation practices may not lead to sustainable outcomes (Millennium Ecosystem Assessment 2005).

Many human populations in low-income regions depend directly on natural resources for survival (Hutton and Leader-Williams 2003). This is true in El Salvador and Nicaragua, where residents of coastal communities generate income from the extraction of marine resources, including fish, mollusks, and the eggs of critically endangered hawksbill sea turtles (*Eretmochelys imbricata*). High human population densities in many coastal areas and increasingly scarce resources place additional pressure on these species and threaten the ability of future generations to meet their needs. Indeed, human actions directly and indirectly affect hawksbill population dynamics, primarily through egg consumption, incidental capture in artisanal fisheries,

and development of nesting habitat. Likewise, hawksbill population dynamics directly and indirectly influence human populations via the amount of eggs available for sale and conservation policies targeted at the reduction of threats to hawksbills that regulate human activities, such as regulations on the extraction of marine resources. Despite the complex interactions and feedback between human and natural systems, traditional policies and management practices tend to recognize one component of the system (i.e., ecological or social) while eclipsing the other, which can undermine their long-term sustainability (Ostrom 2009). There is an urgent need to examine how these systems interact and the impacts on hawksbill nesting ecology, conservation policies, and human wellbeing in El Salvador and Nicaragua.

RESEARCH OJBECTIVES

The purpose of my research is to better understand the nesting ecology and interactions between local and international priorities for hawksbill conservation in El Salvador and Nicaragua, where >90% of eastern Pacific hawksbill nesting occurs. In the first study, I used naturalistic inquiry to the examine the local realities of impoverished coastal residents who share habitat with hawksbills in El Salvador and who rely on hawksbill eggs as an important subsistence resource. In this context, I discussed the implications of the disparities between these realities and international priorities for hawksbill conservation and community development in El Salvador and other low-income regions. In the second study, I investigated nest-site selection by hawksbills in El Salvador and Nicaragua to provide a more comprehensive understanding of regional

variation in this species and to elucidate the potential consequences of hawksbill egg relocation to protected hatcheries in this region. In the third study, I analyzed thermal profiles of nest environments and estimated sex ratios and physical condition of hatchling hawksbills under natural and artificial conditions in El Salvador and Nicaragua. Based on these findings, I examined whether behavioral plasticity in this species is likely to compensate for forecasted climate change and what the role of egg relocation may be as an adaptation strategy.

CHAPTER II

CONNECTING INTERNATIONAL PRIORITIES WITH HUMAN WELLBEING IN LOW-INCOME REGIONS: LESSONS FROM HAWKSBILL TURTLE CONSERVATION IN EL SALVADOR*

OVERVIEW

Hawksbill turtles (*Eretmochelys imbricata*) are highly endangered in the eastern Pacific Ocean, yet their eggs continue to be an important subsistence resource for impoverished coastal residents in El Salvador. In this study, we use naturalistic inquiry to explain the realities experienced by coastal residents who share habitat with hawksbills in El Salvador, and then suggest implications of the disparities between these realities and international priorities for hawksbill conservation and community development in El Salvador and other low-income regions. To provide a context for understanding hawksbill conservation and its implications for similar challenges related to conservation and wellbeing, we first summarize the conservation context, including the emergence of sea turtle conservation in El Salvador. We then describe our naturalistic approach, including the ethnographic methodology for this study. Finally, we detail the analysis of interviews conducted with *tortugueros* (i.e., local sea turtle egg

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collectors), to help explain how hawksbills fit into local realities. Our results demonstrate that, from the perspective of *tortugueros*, (1) the primary importance of hawksbills is the economic value attached to egg sales, but there exists a deeper connection to local culture; (2) egg purchase by hatcheries is a socially just conservation strategy that benefits both hawksbill and human wellbeing; and (3) opportunities for local residents to participate in decision-making regarding sea turtle conservation are limited, and should be increased. We argue that harmonizing international conservation priorities with local community development realities is one path towards simultaneously contributing to long-term sea turtle recovery and human wellbeing in low-income regions.

INTRODUCTION

Sea turtles capture contemporary interest both at international and local levels. Because people consider sea turtles to be charismatic megafauna, they are perceived to have high intrinsic value (Witherington and Frazer 2003) and attract significant public attention (Campbell 2003). The complex life cycles of sea turtles and their pressing conservation status draw interest from the international conservation community, such as the Marine Turtle Specialist Group of the International Union for Conservation of Nature (IUCN) and many internationally oriented institutions. At the same time, sea turtles often are viewed as a subsistence resource in low-income regions (Thorbjarnarson et al., 2000), which can be rooted in cultural heritages (Nietschmann 1973; Morgan 2007). The divergence of these perspectives fails to exploit potential synergies between

local culture and sea turtle conservation, and threatens the viability of existing conservation strategies, including sea turtle egg protection, at both international and local levels.

In this paper, we identify and clarify the implications of discrepancies between local realities and international priorities for hawksbill sea turtle (*Eretmochelys imbricata*) conservation and community development in El Salvador. To provide a context for understanding hawksbill conservation in El Salvador and its implications for other challenges related to conservation and wellbeing, we first draw from the historical record to describe how sea turtle conservation, particularly hawksbill conservation, emerged along the Salvadoran coast. Second, we describe our naturalistic approach to the project, including the ethnographic methodology. Third, we provide detailed analysis of interviews with *tortugueros* (i.e., local sea turtle egg collectors), to help explain how hawksbills and their conservation fit into realities experienced by local residents. Finally, we discuss what our results tell us about the implications of differing international and local priorities for hawksbill conservation and human community development. We argue that hawksbill conservation in El Salvador illustrates the importance of integrating local realities with international conservation priorities in order to simultaneously support long-term sea turtle recovery efforts and human wellbeing in low-income regions.

Conservation Context

Conflict over sea turtle conservation illustrates one of today's greatest

conservation challenges. It requires difficult decisions regarding appropriate levels of resource allocation for protection and management of ecosystems, landscapes, habitats, and species (White et al., 2009; Peterson et al., 2013). Although most biodiversity conservation contexts are shaped by conflict, publications that list crucial priorities (i.e., Sutherland et al., 2009), deal with conflict only marginally and superficially. When conflict is considered, recommendations typically involve trying to eliminate or resolve it through education, financial compensation, and/or local control (Peterson et al., 2013). Although these approaches are valuable additions to conservation efforts, they are rarely envisioned as more than tools to enable policy makers to respond to relatively superficial interests. Numerous studies grounded in critical theoretical perspectives such as political ecology (Campbell 2007) and science and technology studies (Henke and Gieryn 2008; Yearly 2008) indicate that a complex array of experiences, values, beliefs, and social power frame biodiversity conservation. Still, conservation biologists continue to seek a world where conservation policies "are based on science, not emotion" (Shine 2011, p. 6; Peterson et al., 2013). This simplistic view of biodiversity conservation is counterproductive, for it blinds its adherents to social and political dimensions that will determine what policies are developed, followed, and enforced (Peterson et al., 2007; Francis and Goddman 2010). Hawksbill conservation in El Salvador demonstrates the complex socio-political landscape that conservationists must negotiate. Although hawksbills' international visibility and perceived charisma have driven adoption of strong protective policies, enforcement of those policies requires at least a minimal level of support from local human communities.

Sea turtles are long-lived, late-maturing, and highly migratory species that frequently cross jurisdictional boundaries while travelling between foraging areas and nesting beaches, which can be separated by entire ocean basins (Nichols et al., 2000b; Luschi et al., 2003). Seven species of sea turtles exist worldwide, most of which have global distributions. They include the olive ridley (*Lepidochelys olivacea*), green (*Chelonia mydas*), loggerhead (*Caretta caretta*), flatback (*Natator depressus*), leatherback (*Dermochelys coriacea*), Kemp's ridley (*Lepidochelys kempii*), and hawksbill turtles. All species, except the flatback, are listed on the IUCN *Red List of Threatened Species* as Critically Endangered, Endangered, or Vulnerable on a global scale.

Historically, hawksbills were prized for their ornate shells that were collected to fabricate a multitude of items for the tortoiseshell trade, including combs and jewelry; however, centuries of exploitation have reduced hawksbill populations by more than 80% worldwide and justified their classification as Critically Endangered by the IUCN (Mortimer and Donnelly 2008). Despite evidence that the listing was based on rigorous scientific investigation, the IUCN decision sparked harsh criticism that highlights the political and economic dimensions of conservation (Campbell 2012). Dramatic declines are evident in the eastern Pacific Ocean, where hawksbills were once common from Mexico to Ecuador (Cliffton et al., 1982), but now are among the world's most critically endangered sea turtle populations (Seminoff et al., 2003; Wallace et al., 2011) with only 200–300 females nesting annually along the region's 15,000 km coastline (Gaos et al., 2010). Because roughly 45% of all known nesting for the species occurs along the 300

km coast of El Salvador, conservation efforts targeting hawksbills along the Salvadoran coast have been identified as a top priority (Liles et al., 2011). Despite the extensive abatement of the tortoiseshell trade in the eastern Pacific, egg consumption, incidental capture in fisheries, and coastal development continue to threaten hawksbill survival in the region (Gaos et al., 2010).

In low-income regions such as El Salvador, the direct use of natural resources remains an essential livelihood strategy for many people (Hutton and Leader-Williams 2003; Mazur and Stakhanov 2008) particularly in rural and coastal areas where poverty is most acute (Lehoucq et al., 2004). As the smallest and most densely populated country in Central America, marine resources in El Salvador are commonly overexploited, exacerbating the vulnerability of historically marginalized coastal residents (Gammage et al., 2002). Because the need to satisfy immediate needs often takes precedence over concern for dwindling natural resources, virtually unregulated extraction contributed to the collapse of locally important resources (JICA and MAG 2002; Catterson et al., 2004) and is compromising future generations' ability to use these resources to meet their basic needs. For example, persistent overfishing contributed to the sharp decline in shrimp and Pacific seabob exports from $40 million in 1995 to less than $4 million in 2007 (FAO 2009). Additionally, the reduction of public-sector budgets restricted the ability of state authorities to deliver services, monitor infractions, and enforce environmental laws, allowing further degradation of coastal ecosystems (Gammage et al., 2002). This is particularly problematic when the declining resources are endangered species, such as hawksbills along the Salvadoran coast.

Cooperation among nations located within the geographical range of hawksbills is essential for coordinated conservation actions to minimize threats in the eastern Pacific. However, the resulting multi-scalar management strategies often emerge from international agendas that may conflict with local priorities, particularly in resource-dependent areas of low-income regions. Priorities of the international conservation community, as exemplified by the Marine Turtle Specialist Group, often center on biological aspects and needs of hawksbills, whereas local priorities of coastal residents tend to focus on socio-economic development and needs of human communities. Focusing on biological dimensions of hawksbill conservation can result in local realities (i.e., context-specific social and environmental conditions) of coastal residents being deemphasized or excluded entirely from nest protection strategies supported by the international conservation community.

Hatcheries and Direct Payments for Conservation Outcomes: Biological and Social Dimensions

The ubiquitous use of hatcheries for incubating sea turtle eggs worldwide underscores their importance as a tool for local sea turtle conservation (Mortimer et al., 1993; Marcovaldi and Marcovaldi 1999b; Formia et al., 2003; Garcia et al., 2003; Chacon-Chaverri and Eckert 2007; Patino-Martinez et al., 2012a). Hatchery design and construction vary depending on a number of factors, such as desired capacity and availability of funds and building materials. Conservation organizations and groups have attempted to standardize hatchery operations by developing guidelines that detail proper

methodologies for hatchery construction, clutch extraction and relocation, and hatchling release (Eckert et al., 1999; Chacon et al., 2008). Despite these efforts, hatcheries often are criticized for operating under poor management practices that produce inadequate biological processes and outcomes (Prichard 1980), such as low hatching success (Boulon et al., 1996), biased sex ratios of hatchlings (Morreale et al., 1982), and increased hatchling mortality (Pilcher and Enderby 2001). Indeed, the Marine Turtle Specialist Group has made its position regarding hatchery use unequivocal: "relocation of eggs to a protected hatchery site should be undertaken only as a last resort and only in cases where in situ protection is impossible" (Mortimer 1999, p. 175). By utilizing proper methodologies throughout the hatchery implementation process, however, many of the undesired biological outcomes can be avoided or successfully mitigated (Marcovaldi and Marcovaldi 1999b; Kornaraki et al., 2006; Patino-Martinez et al., 2012b).

While we understand the potentially negative biological outcomes associated with manipulation of sea turtle eggs and hatchlings, we contend that the value of hatcheries extends beyond their immediate biological output. The widespread implementation of hatcheries in low-income regions speaks to their ability to garner local support for sea turtle conservation, and to open the conservation enterprise to participation by local residents. Initially, hatchery operations can be linked to human wellbeing via egg purchases from *tortugueros*, where coastal residents are rewarded for active participation in nest protection and thus become joint owners of conservation successes. This opens possibilities for more sustainable benefits, where direct payments

for conservation outcomes have been shown to be an effective motivator for behavioral change, particularly for initiatives to protect sea turtle nests (Ferraro and Gjertsen 2009). For example, if the desired outcome is to protect a sea turtle nest, the sea turtle nest is purchased directly from the "seller", or in this case the *tortuguero* that found the nest, for protection. Direct payments for conservation often are more cost-effective than regulatory-based initiatives in dispersed nesting environments (Gjertsen and Stevenson 2011) and offer a socially just strategy for nest protection that recognizes human need. Some observers may conclude that these direct payments for conservation outcomes related to sea turtle eggs placed in hatcheries are yet another example of the universal merits of re-presenting ecosystem functions and related biodiversity as ecosystem services to humanity. Ehrlich and Ehrlich (1981) proposed this re-presentation in order to highlight the importance of ecosystem functions and related biodiversity to humanity (Peterson et al., 2010). It was not until Costanza et al. (1997) "conservatively estimated" the economic value of 17 ecosystem services for 16 biomes at US$16–54 trillion annually (1994 dollars; mean = $33 trillion annually), however, that ecosystem services became a dominate conservation theme. Certain ecosystem services undoubtedly were far more cost-effective than technological solutions to environmental problems (Daily and Ellison 2002; Pires 2004), and conservation biologists began to perceive neoliberal economics and politics (Aune 2001; Harvey 2005) embodied in the services concept as a panacea for conservation conundrums (see Büscher 2008; Child 2009; Redford and Adams 2009). Chan et al. (2007), with Paul Ehrlich himself as a co-author, concluded there are numerous situations in which conservationists should argue for conservation

for biodiversity's sake alone rather than for its direct benefits to humanity. Several other conservationists soon provided critiques of uncritical reliance on ecosystem services—and neoliberal economics generally—as a basis for biodiversity conservation (Vira and Adams 2009; Walker et al., 2009; Peterson et al., 2010; Büscher et al., 2012).

Moving beyond the neoliberal economic perspective that grounds the concept of ecosystem services, the marginalization or social exclusion of *tortugueros* and other local residents from decision-making regarding marine resource use has far-reaching implications for conservation. Because the extraction of wild natural resources is a high-risk endeavor that is prone to uncertainty and seasonal fluctuations, coastal residents in low-income regions tend to pursue diversified livelihood strategies that spread risk of failure across more than one income source (Allison and Ellis 2001). For example, coastal residents are often involved in different ventures that include, but are not limited to, sea turtle egg collection, to reduce the risks of resource variation. This mobility across multiple resources facilitates interactions between coastal residents and diverse economically and/or biologically important resources, which not only plays a fundamental role in local economies (Béné et al., 2009) but also offers opportunities for enhanced conservation of myriad marine species. While we understand that local participation is not a panacea for conservation (Almeida and Mendes 2007), we consider the engagement of local residents in conservation an essential step towards achieving sustainable solutions.

We recognize that the Global Strategy for the Conservation of Marine Turtles of the Marine Turtle Specialist Group (1995, p. 14) states, "where management projects

have excluded rural people as agents in conservation, unsustainable management plans have resulted". The report suggests developing "marine turtle recovery plans that address and include the political, economic, and cultural conditions of coastal people affected by management actions and promote, where appropriate, the active participation of these communities in marine turtle conservation". In practice, however, the Marine Turtle Specialist Group recommendations exclude *tortugueros*, who are likely the most knowledgeable members of local communities regarding sea turtles, from turtle conservation activities. One recommendation, for example, directs conservationists to conduct beach patrols to deter "poachers" and to disguise nests by erasing tracks and smoothing out the area to match its surroundings (Boulon 1999).

Natural resource policy and management strategies strongly reflect the socio-political context in which they were created and to which they are intertwined (Yaffee 1994). Because many threats to species are rooted in the cultural, economic, or political dimensions of a situation, conservation actions that focus only the species' biology invite failure (Clark et al., 1994). Therefore, consideration of the political history of El Salvador can give insight into the factors and experiences that shaped Salvadoran society, natural resource use, and sea turtle conservation.

Emergence of Sea Turtle Conservation in El Salvador

In El Salvador myriad socio-political processes and events shaped natural resource use and conservation over the last several centuries, driven in large part by land acquisition for coffee production and the 12-year (1980–1992) civil war between the

oligarchy-military alliance and displaced *campesinos* (i.e., local, small-scale farmers). In 1880, coffee overtook indigo as the country's leading export, which prompted the Salvadoran government to pass laws eliminating collectively held lands; communal and public lands then were divided and sold to large-scale coffee and indigo estates in an effort to replace sustenance farming with the production of cash crops (White 2009). Coffee and related exports yielded enormous profits and land quickly became concentrated with a few families, allowing them to diversify their investments and venture into other economic sectors, such as real estate, commerce, and tourism (LeoGrande and Robbins 1980). Between 1979 and 1980, the Farabundo Marti National Liberation Front (FMLN) formed with the purpose of redistributing power and resources to those members of society that had been repressed by the traditional political and economic structure. In 1980, conflict between the oligarchy-military alliance and the FMLN exploded in a civil war that lasted 12 years.

At the signing of the Peace Accords in 1992, the civil war had resulted in approximately 75,000 deaths and over 1 million displaced persons (i.e., 1/5 of the total population). The war impelled many families to emigrate from the highlands and settle in coastal areas (Gammage et al., 2002) where they survived on the exploitation of wild natural resources, such as fishing, mollusk extraction, and sea turtle egg collection. High poverty levels are common along the 300 km Salvadoran coast, with most households lacking potable water and waste collection services, discontinuing education at middle-school level, and earning monthly incomes of $100 (Castillo and Quezada 2010).
As human settlements have increased in coastal areas and overexploitation of sea turtle

eggs has become increasingly evident, conservation initiatives to address threats to sea turtles and their habitat have sometimes ignored dramatic divergence between the realities experienced by local and global participants. Four of the seven sea turtle species nest along the Salvadoran coast—the olive ridley, green, leatherback, and hawksbill. The olive ridley is the most abundant sea turtle in El Salvador, followed by the green, hawksbill, and leatherback, which combined lay approximately 9000–13,000 nests annually in El Salvador (Vasquez et al., 2008). In 1975, the first project targeting sea turtle conservation was initiated at Barra de Santiago beach with funding from the Ministry of Agriculture and Livestock (MAG) (see Table 1 for chronology of sea turtle egg protection and hatchery management in El Salvador). This project employed the first use of hatcheries to protect and incubate eggs; in 2013 hatcheries remain the primary method of nest conservation along the coast of El Salvador. High human density and acute poverty in coastal areas have made the protection of sea turtle nests in situ (i.e., original site of deposition on the beach) infeasible at most beaches. Nearly 100% of eggs deposited by sea turtles are extracted by approximately 4000 *tortugueros* and are sold to either hatcheries operated by local NGOs for protection (flat rate = $2.50 per dozen eggs) or the market for consumption (mean = $2.78 [range = 2.10–4.00] per dozen eggs) (Romanoff et al., 2008). By purchasing eggs from *tortugueros*, hatcheries provide an alternate economic incentive to sale for consumption and thus have gained acceptance among coastal communities. Although hatcheries vary in size and quality, most are approximately 100 m^2 with a capacity of ca. 200 sea turtle nests, made from local materials, and placed in the broad sandy nesting areas of beaches. In 2012, 37 hatcheries

operated along the coast of El Salvador that protected nearly 1,700,000 eggs and obtained an overall hatching success of 88%, yielding over 1,450,000 hatchlings (MARN 2013b). Most hatcheries are project-funded, which means they are economically unsustainable and require external funding for operation. Additionally, funding is typically provided on an annual basis and is unstable. Inconsistent funding has led to dramatic variations in the number of hatcheries that operate and the number of eggs incubated annually.

Since the Peace Accords were signed in 1992, the Salvadoran government has established a legal framework to provide sea turtles protection through the ratification of international agreements, such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; República de El Salvador 1986) and the Convention on Biological Diversity (República de El Salvador 1994a). National legislation recognizes and extends protection to sea turtles as endangered species (República de El Salvador 1994b, 1997) and attempts to mitigate the incidental capture of sea turtles in fisheries (República de El Salvador 2001, 2007). Additionally, *tortugueros* were required to donate an average of one dozen eggs per nest, which typically contain 100 eggs, to the local hatchery (if one existed); the remaining eggs then could be legally sold for consumption (MAG 1997). Despite this requirement, few eggs were protected (Vasquez et al., 2008), which hampered El Salvador's ability to ratify the Inter-American Convention for the Protection and Conservation of Sea Turtles (IAC). To address this problem, the Salvadoran government prohibited the collection and sale of sea turtle products, including eggs, for purposes other than conservation (República

de El Salvador 2009), which further elevated the role of hatcheries as a means of encouraging statutory compliance. According to the Ministry of the Environment and Natural Resources (MARN), the decision to develop and approve the moratorium stemmed from national and international pressure and was substantiated by (1) Chapter 17 of the Central American Free Trade Agreement (CAFTA-DR) with the USA, (2) a rapid assessment conducted by the United States Agency for International Development (USAID) that claimed *tortugueros* earned less than $200 annually from the sale of eggs (Romanoff et al., 2008), and (3) a survey of sea turtle nesting beaches conducted by a local conservation organization and the University of El Salvador that concluded nearly 100% of sea turtle eggs deposited along the Salvadoran coast were collected and sold for human consumption (Vasquez et al., 2010). If *tortugueros* earn $200 annually (which is likely underreported; Gavin et al., 2010) and the average annual household income for *tortugueros* is estimated at $1230 (Castillo and Quezada 2010), then sea turtle egg sales represent a substantial 16% of their annual household income.

For decades, the occurrence of hawksbill nesting along the coast of El Salvador was unclear due to inconsistent data, much of which were anecdotal and inconclusive. Some researchers claimed that existing records of nesting hawksbills were incomplete and could not be confirmed (Hasbun and Vasquez 1999; Arauz 2000), while others stated that low-density hawksbill nesting occurred 30 years ago on Salvadoran beaches, but no longer occurred in modern times (Mortimer and Donnelly 2008). Recently, however, nesting by hawksbills in El Salvador has been confirmed at levels critical to the continued survival of the population in the eastern Pacific (Gaos et al., 2010; Liles et

al., 2011).

METHODS

Naturalistic Inquiry

Guba's (1978) classic treatise identified the extent to which the researcher manipulates some phenomenon in order to study it; and the extent to which categorical constraints are placed on outputs as distinguishing characteristics of scientific inquiry. Naturalistic inquiry, with its aversion to manipulation of a study context, and its open acceptance of any sort of outputs, is an excellent fit with our attempt to better understand the multiple realities experienced by human residents of coastal areas, to explain how those realities shape interactions with hawksbills, and to begin to understand motivations related to hawksbill conservation in El Salvador. Given our objective, we sought to exert minimal manipulation as we began to develop an integrated understanding of local community realities and hawksbill conservation.

Naturalistic inquiry enables discovery of the many ways personal experiences and their social contexts shape people's constructions of reality (Lincoln and Guba 1985). The multiple realities of local residents who interact with hawksbills must be viewed holistically, as they are inseparable from the contexts in which they developed. In addition, fully immersing at least one member of the research team in the study area for prolonged periods of time facilitates learning from the residents how to interpret their realities while at the same time detecting both intentional and accidental fabrications. Further, persistent observation during these years facilitates understanding of tacit

knowledge and aids interpretation of interview data. We are not so naive as to think our inquiry is not influenced by our own values, and the criteria suggested for judging naturalistic inquiry, such as transferability, dependability, and confirmability, have guided us through challenging decisions regarding our ability to interpret events that occur in coastal areas.

Ethnographic Approach

Since the discovery and systematic documentation of substantive hawksbill nesting along the Salvadoran coast in 2008, researchers have partnered with local egg collectors to conduct participatory research and conservation activities at the nation's three primary hawksbill nesting sites: Los Cobanos Reef Marine Protected Area (Los Cobanos), Bahía de Jiquilisco-Xiriualtique Biosphere Reserve (Bahía), and Punta Amapala (Fig. 1; Liles et al., 2011). Our research team has participated in this effort. Liles spent most of the past seven years (2007–2013) engaged in multi-sited ethnographic research (Coleman and von Hellerman 2011) in El Salvador. He immersed himself in local community contexts with primary marine resource users and at the national level with decision-makers. In 2007, he made initial contacts with *tortugueros* and community leaders at 64 beaches. During that year, local informants explained to him that nearly 100% of hawksbill eggs were collected by *tortugueros* and sold legally in local markets for consumption. In 2008, Liles secured funding to initiate hawksbill nest conservation activities, including the purchase of eggs from *tortugueros* for protection in hatcheries, which contributed to gradual development of greater rapport

with local residents. As relationships deepened and trust strengthened, *tortugueros* began to initiate conversations about sensitive topics such as sea turtle egg consumption and their views of conservation policies in general.

In 2009, Liles returned to the USA for four months. Along with members of the coastal communities where he had lived and worked, Liles was surprised when the Government of El Salvador announced a permanent moratorium on the collection of sea turtle eggs for purposes other than conservation. When Liles returned to El Salvador, most of the *tortugueros* were nervous about interacting with him, especially regarding the now illegal sale of turtle eggs for human consumption. Some members of the community remained willing to work with Liles, and explained that lack of forewarning about the moratorium, combined with Liles' absence at the time it was announced, led some individuals to fear that Liles, along with other conservationists, had betrayed their trust. Since 2010, Liles has focused on rebuilding relationships among conservation organizations, government agencies, and *tortugueros* that were damaged and/or dissolved by the moratorium.

In preparation for conducting this analysis, Liles spent over 2750 hours in the three primary Salvadoran hawksbill nesting sites. During this time, he has taken more than 300 pages of field notes, conducted hundreds of informal interviews with key informants and residents, and participated in over 100 night patrols with *tortugueros* searching for hawksbill eggs. These close encounters with *tortugueros* provided a forum for observing their interactions with hawksbills and with other *tortugueros* and increased the likelihood of obtaining authentic information. Other members of our team have

visited and worked with local residents during this time, but remain outsiders. We follow Hammersley and Atkinson's (2007) guidance on selecting ethnographic informants, which means that informants are purposively selected based on their insights, knowledge, roles, and willingness to discuss their experiences. Beginning immediately upon his return following the moratorium on the collection of sea turtle eggs for consumption, Liles identified key informants to facilitate semi-structured interviews with *tortugueros*. The reason for conducting these interviews was to learn as much as possible about the *tortugueros*' experientially based relationship with hawksbills and their conservation. We selected *tortugueros* because, more than any other group of people, their day-to-day existence connects with turtles.

Collection and Analysis of Interview Texts

We constructed open-ended questions (Peterson et al., 1994) in Spanish, and Liles conducted interviews with 34 *tortugueros,* all of whom had long-term experience collecting hawksbill eggs from the three primary hawksbill nesting sites (Fig. 1), to help understand how they prioritize hawksbills and their perspectives towards hawksbill conservation in El Salvador. Our ethnographic approach enabled us to perceive how personal experiences and their social contexts shaped informants' perceptions of reality and how language was used to construct that reality (Lincoln and Guba 1985). To identify potential informants at each site, we confided in local contacts with whom we had developed long-standing relationships of trust that had withstood the shock of the 2009 mandate. These local contacts used their established relationships with other

tortugueros from their communities to arrange interviews. Informants chose the location of the interviews as a means of transferring control from the researcher to the informant in an effort to increase trust and promote a relaxed environment. By fully immersing ourselves in the context of the study area, we learned from informants how best to interpret their realities (Peterson et al., 2002). We used a variety of techniques to manage issues of accuracy with the data, including triangulation, informant validation, clarification questions, and continual movement between data collection and analysis (Lincoln and Guba 1985). To ensure accurate data transcription, we requested consent from informants to record the interviews. All fieldwork was conducted by Liles in accordance with Institutional Review Board requirements (IRB Protocol #2009–0277) at Texas A&M University and a native Salvadoran skilled in English transcribed and translated all interviews.

We conducted a thematic analysis (Peterson et al., 1994) of the transcribed text and used data from the published literature and unpublished reports to supplement field notes and interview transcripts. Whenever possible, we used the informants' own words to describe their perspectives and experiences.

RESULTS

Three themes emerged that were common across all interviews (see list), which we discuss in detail below.

(1) All informants valued hawksbills primarily for the economic value attached to egg sales, but many also alluded to deeper connections to local culture.

(2) All informants identified egg purchase by hatcheries as a socially just conservation strategy that unified hawksbill nest protection with human wellbeing.

(3) Most informants stated that opportunities for local residents to participate in decision-making regarding sea turtle conservation are limited and biased towards elite, non-residential interests. They suggested involvement opportunities for local residents should be increased.

The Value of Hawksbills

All interviewees identified the economic value of eggs as the primary value of hawksbills. Because poverty is rampant along the Salvadoran coast and employment options limited, coastal residents are invariably linked to the natural resources that surround them. Whether consumed locally or extracted and sold for income, the livelihoods of coastal community members depend on resources from their local environment for essential goods and services, including hawksbill eggs. One *tortuguero* from the Bahía commented:

> To make our community whole, we live off of fishing, mangrove cockles, and the extraction of clams. But in the hawksbill nesting season we depend on the turtle. One goes to the beach and finds a clutch of eggs and with that, you now have enough to buy food for your children and siblings.

This statement demonstrates how resource dependence shifts according to season, which can make these communities particularly vulnerable to resource availability and seasonal fluctuations during certain times of the year. Traditionally, hawksbill egg collection buffered coastal residents from the economic impacts of such transitions and

fluctuations, particularly during the winter (i.e., rainy season), which coincides with the peak of the hawksbill nesting season (Liles et al., 2011). Concerned about the implications of the moratorium on the sale of sea turtle eggs for consumption during these seasonal shifts in resource abundance and weather, one informant stated:

> And in the winter? I explained to the Ministry [of the Environment and Natural Resources] that in the winter the storms cause commerce to decline—mangrove cockles, fish—when you cannot go out [to fish] because of the north winds, the strong, tropical storms, you go to the beach, find turtle [eggs], and on that you maintain yourself.

Informants from all three sites explained that hawksbills typically are preferred by *tortugueros* because they lay more eggs than the other species of sea turtles, which means higher profits. Comments such as those of an egg collector from Punta Amapala were common:

> Hawksbills always lay more [eggs]; olive ridleys lay few so it is more advantageous to search for nesting hawksbills—produces more money for the family.

Although all informants highlighted the economic value of eggs, many *tortugueros* described the relationship between hawksbills and egg collectors as more complex and profound than might be expected. Most spoke of hawksbills with a reverence that reflected a deeply held respect and appreciation. In describing his relationship with hawksbills, one informant, who is both a *tortuguero* and community leader in the Bahía, embodied the comments of many other interviewed *tortugueros*:

> For me, [hawksbills] have great value because they relieve poverty. They relieve the poverty of coastal communities, those that live along the edge of the ocean. [They provide] a great amount of assistance to maintain families, because we are going from poor to poorer. There is the person that goes to the beach in the evening without so much as 5 cents, he finds a turtle [nest], and come morning he has between $12 and $15. Now he can provide for his family. They are

> content. He returns to the beach; if he does not find a turtle that night, he will find one another night. The primary value that I put on a turtle is that it favors the homes of the poor. For that reason, it has great value to me.

The relationship a *tortuguero* has with hawksbills can transcend economic terms with roots firmly established in tradition. Although some informants spoke indirectly about tradition and culture, one *tortuguero* from Punta Amapala acknowledged it directly:

> There are people that now do it [search for nesting hawksbills] as a custom, going every night . . . whether they find a turtle or not, it is a tradition.

The habitual act of walking the beach each night demonstrates that the connection between hawksbills and *tortugueros* can be as much of a process as an outcome. The way some informants alluded to the similarities between the life cycle of turtles and humans, and the suffering experienced by both, illustrated an empathic bond our informants claimed with the hawksbills. When asked about his thoughts on hawksbill conservation, one *tortuguero* from Los Cobanos responded:

> Think about how much a turtle suffers to become an adult; from its birth it has to swim as a hatchling and at 10 or 15 or 20 years old it has to come back to nest. It is suffering to pass through that large trajectory and then, perhaps, it might die in its youth. The life of a turtle is like the life of a human—it is of great value and must be conserved and protected.

Tortugueros are often portrayed by biologists as having very simplistic and superficial interactions with sea turtles, usually driven by short-term self-interest with little concern for the wellbeing of the turtle (Shaw 1991; Campbell 2000, 2002). Most *tortugueros* interviewed for this study demonstrated that their relationships with hawksbills were much more complex and based on respect and appreciation. Although informants identified the economic value of hawksbill eggs as essential, they also expressed a tension between satisfying their immediate economic needs and their desire

to conserve the species.

Egg Purchase by Hatcheries Connects the Needs of Hawksbills and Humans

All informants identified egg purchase by hatcheries as a socially just conservation strategy that benefited both hawksbill populations and human wellbeing. Because coastal community members are tied to local natural resources, they are particularly vulnerable to policy decisions affecting the use and management of those resources. In Los Cobanos and Punta Amapala, many *tortugueros* commented on the economic hardship created by the moratorium on the sale of sea turtle eggs for consumption due to the absence of operating hatcheries, which essentially outlawed the legal sale of hawksbill eggs. What was once an important source of legal income for many coastal families was now prohibited. Informants emphasized their fear of economic uncertainty and called for alternative sources of employment from the governmental or non-governmental organizations to lessen the impact of the moratorium:

> Sincerely, I say, that for me the ban has an impact. I do not look at it negatively; I look at it positively because it is about the protection of sea turtles. What you do see is that it has had an impact and has upset the poor members of the population, the communities that live in this sector, because as egg collectors when the hawksbill nesting season arrives, many of our families earn money to provide for our children [by collecting and selling eggs]. Now with the ban, we have not received any alternatives and although they [the government] say that they are coming, we still do not have a [material] reality to resolve this situation. But the part of the ban being about the conservation, management, and taking care of sea turtles, that is excellent. But we feel the economic void and many families feel abandoned. If the Ministry [of the Environment and Natural Resources] or other institutions would give some alternative solutions to our families, then we believe that the ban would be good.

The need for alternative sources of income to replace egg sales for consumption was echoed by all informants. They suggested implementation of a variety of alternatives, such as aquaculture, artificial reefs for hook-and-line fishing, and tourism, to help replace the income-loss resulting from the moratorium. However, when asked if these alternatives would prevent hawksbill eggs from being collected and sold illegally for consumption, all informants said that they would not. They also noted that alternative income sources needed to be appropriate to local economic realities. Referring to an article that came out in a local newspaper stating that the government would be providing chicken coops to *tortugueros* as an alternative to collecting and selling eggs, a *tortuguero* from Punta Amapala stated:

> To change a person's way of life and say that now they cannot extract sea turtle eggs from the beach, it is necessary to give that person another type of employment. Because one person can change if you give him a chicken coop . . . because that way he can maintain himself with six or seven of those little animals. It would work for him. But they [the government] will not give a coop to everyone along the beach. Not to everyone. If he [motioning to another egg collector] stops collecting eggs, three more will come in and take his place, because we have a dense population . . . him alone [motioning again to the egg collector] has 6 kids. That is why it [chicken coops] will not work.

Informants stated explicitly that if nests were not purchased for protection, they would be sold illegally for consumption; no nest will be intentionally left where it was laid on the beach because if one *tortuguero* does not extract it, another will:

> It is very rare that a hawksbill comes up to nest and only the person that collects the nest sees it. There are always others who see who collected it. So, if I leave it there, because for me it is illegal to take it, another person will come that night or later on and will harvest and take it, whether to consume it himself or to sell it illegally. That will always happen. To have 12 dozen turtle eggs at $3.00 per dozen that he'll be paid for them, how much did he make, eh? That is how people think, in hiding and selling a dozen eggs to such a place or to such a family. If there is only consumption [as an option for income], you hide them

and you know it is prohibited; people always feel that necessity.

Many informants mentioned the struggle to negotiate tensions between the protection of hawksbill eggs and the economic benefits generated from egg sales. The solution to this dilemma as offered by all informants was the implementation of protected hatcheries. These hatcheries would purchase the eggs from *tortugueros*, thus providing economic relief for the human population. Hawksbill eggs would be incubated in hatcheries, from where the hatchlings that were produced would be released to perpetuate the cycle.

> They [hatcheries and egg purchase] are two things that must be carried out side-by-side, they must be carried out side-by-side because if they are not, one of the two things will be left behind; and that one thing that is left behind will be the hawksbill because the economic situation is always going to be difficult. But by having hatcheries that purchase the eggs from collectors, we can achieve both objectives [hawksbill conservation and human wellbeing] at the same time.

Some informants had hatcheries operating in their communities, while others did not. When one *tortuguero* that lived in a community with a hatchery was asked what would happen if the hatchery did not exist, he answered:

> In this area, if there was not a hatchery that was buying hawksbill eggs right now, the *tortuguero* would leave. He would take the eggs and go sell them by the dozen [for consumption] because he would have to get money to live.

Other options, such as increased law enforcement by police, were not likely to result in nest protection:

> Of course the moratorium can work here; that's why the community has been requesting that a hatchery be built. [But] if there is no hatchery, it won't work. [Expecting] the police to come [patrol] is dreaming—an illusion.

In an effort to deter the illegal sale of eggs on local markets, the Salvadoran government placed a penalty of up to five years in prison for a person found with turtle

eggs that were not destined for conservation purposes. Although many *tortugueros* mentioned that they feared being caught with eggs by the police, they felt that it was extremely unlikely. When asked how the threat of law enforcement by local police affected *tortugueros*, one informant from Punta Amapala replied:

> The authorities here, the agents of authority like the police, we don't have their true support because they don't have dedication; they don't have the adequate capacity to, let's say, support, help, or protect hawksbills. They don't have it. I know that here there are only eight policemen available and for all the communities that they have to attend to here, they are not able to handle all of the work they have to do. The vehicles that they drive to go from one place to another are often deficient; sometimes they don't have gasoline, or the personnel aren't around because they are in one place or another. So there are many demands that they can't cover at the time that you need them. They just can't handle it all.

Such statements by *tortugueros* indicate their awareness that Salvadoran authorities are unlikely to enforce laws designed to protect hawksbills, often due to lack of resources and political will. This situation leaves the fate of hawksbill nests resting in the hands of the *tortugueros*, since ultimately they decide whether to sell the eggs for conservation or for consumption. This local reality underscores the power and control *tortugueros* wield in determining the success or failure of hawksbill conservation initiatives in El Salvador and the importance of including them as stakeholders in conservation decision-making processes.

Conservation Decision-making Excludes Local Residents

The success of sea turtle conservation initiatives that use hatcheries as tools for nest protection relies on the direct participation of *tortugueros* and other coastal residents. The long history of hatchery use in El Salvador has fostered relationship

building among *tortugueros*, government agencies, and conservation organizations. The acknowledgement of coastal residents as important stakeholders in sea turtle conservation efforts recognizes and validates local agency in influencing conservation outcomes. As one *tortuguero* put it:

> Each year [sea turtle] numbers decline and we have worked with many institutions to protect and conserve turtles since 1997. Think about how if we hadn't done this since that time, there would be fewer turtles; we are now seeing the results of the hatchlings that we had released back then that are now coming back to nest. So, you can see that sea turtle protection and conservation have a huge impact and keeps them from disappearing here, because if not, in 10, 15, or 20 years our children and nieces and nephews won't experience them.

Active participation by coastal residents in the design and execution of sea turtle projects fosters joint-ownership and promotes resource stewardship. However, *tortugueros*' motivation to protect sea turtles via collaboration with public and private institutions is not unconditional. To exclude local communities from decision-making processes that have outcomes that affect them may jeopardize the relationships of trust and understanding that have been built over decades. Most informants expressed feelings of betrayal at the surprise announcement of the moratorium on the sale of sea turtle eggs for consumption. They were angered that they received no advance communication regarding the decision; instead, they simply heard or read about it through media outlets. Given El Salvador's socio-political history, many viewed the moratorium as another example of government catering to elite interests while sacrificing those of the poor. One stated:

> [Coastal] people are human; although we may be poor, we are human. All of us are humans; we feel and everything the same. It is necessary to communicate with [poor] people during the [decision-making] process, because [the decision] will harm some and not others. Clearly, there is the one that has everything, like

> the [rich] that has, let's say, cattle, property, has a place to live. Then there is the one that doesn't have anything, that is in his little shack and living off of the ocean—that is the one that it harms.

Interviewees suggested that actively involving coastal residents in decision-making processes that will affect them may produce negotiated outcomes that are more likely to be sustained than outcomes forced upon stakeholders. Decisions that are formulated without the participation of those who will be responsible for adhering to them (e.g., *tortugueros*) may not have incorporated local realities. For example:

> They [lawmakers] said yes [to the moratorium] without thinking about the poor that survived [on egg sales], that is the big problem. They didn't think, meditate, about the poorest of the poor that maintained themselves off of that, maintained their children, their home. I am certain that if the [local] communities would have been able to provide ideas then coastal residents would have been more flexible to some sort of negotiation—even if the agreed upon outcome was not exactly what we wanted, at least we would have been able to negotiate.

Some informants also questioned the validity of the decision by the Salvadoran government to prohibit egg consumption, which affects the poor, instead of addressing adult turtle mortality by industrial fisheries, which would affect more powerful interests. Many *tortugueros* claimed that improving regulations on industrial shrimp trawls would reduce the number of adult turtles killed and have much larger conservation impacts than focusing efforts on egg protection. As one respondent put it:

> *Tortugueros*, the poor people, we are the victims. Those that have made large sums of money, the most powerful in our economy, by using the famous bribes to government officials to exploit our resources, it's because of them that the turtles are faced with extinction. And now this moratorium comes that affects all of us, even though we are not to blame for the endangerment of these resources. The maximum authorities should be thinking of how the government has committed enormous errors by permitting the millionaires of the country to do illegal things, inadequate uses of resources, uses of land, and whatever other use that hurts the poor populations. They know that we know and that's why government officials never come to meet with fishers or *tortugueros*. They know

> we will criticize the authorizations that have come down from above to help the rich, so instead they send people to hand out t-shirts and hats, to appease the victims until their term is over.

Overall, informants expressed high levels of distrust in current decision-making processes regarding conservation policy and expressed frustration with perceived corruption within the government. With few exceptions, interviewed *tortugueros* desired more participation in political processes that have a direct influence on their wellbeing.

DISCUSSION

Our informants highlighted the economic value of egg sales as the primary value of hawksbills, but spoke of deeper connections to turtles that transcended neoliberal economics and drew on experiences rooted in local culture. Informants identified egg purchases by hatcheries as a conservation strategy that benefited both hawksbills and human communities, and unequivocally stated that any hawksbill eggs not purchased for protection by conservation initiatives were sold for human consumption. Finally, our informants desired more participation in decision-making regarding sea turtle conservation, which they deemed to be biased towards elite interests.

Divergence of International Priorities from Local Realities

Hawksbills are highly regarded by both the international conservation community and coastal residents in El Salvador; however, local and international priorities concerning hawksbills diverge. Priorities of the international conservation community often center on the biological aspects and needs of hawksbills, whereas local

priorities of coastal residents tend to focus on the socio-economic development and needs of human communities. By prioritizing the biological dimensions of hawksbill conservation, local realities of coastal residents are deemphasized or excluded entirely from nest protection strategies supported by the international conservation community. Examples include pressure to protect eggs in situ and disapproval of payments for conservation outcomes—because they are considered economically unsustainable—such as the purchase of hawksbill eggs for their relocation to hatcheries. To emphasize this point, an influential Marine Turtle Specialist Group member stated:

> To address poaching—I argue that to move the eggs to a new nest cavity 20 feet from its current location works just fine to shut down poachers, they'll never know where to look.

These experts from the international conservation community are pursuing nest protection tactics that appear to ignore the need for coexistence between humans and sea turtles. When our informants analogized the struggles experienced by hawksbills with the struggles experienced by local human residents, they offered the basis for a sustainable conservation strategy with deep links to both human and turtle wellbeing. Considering *tortugueros* as essentially inanimate objects to be "shut down" like an unwanted machine negates the ties they have to sea turtles and invalidates the context within which they live.

Practices such as these foster a false conservationist versus *tortuguero* dualism that promotes a sense of direct competition for resources between the two groups. Situating *tortugueros* as enemies to sea turtles is both a simplistic and inaccurate construction of local reality that fails to acknowledge the underlying contexts in which

egg collection occurs. Advocating a sort of conservation where conservationists compete with impoverished *tortugueros* for resources that support local livelihoods is not only ethically questionable, but also can escalate tensions and provoke latent conflict between international conservation organizations and local residents.

In contrast, both material and symbolic realities of coastal residents dictate local priorities and nest protection strategies that are informed by community concerns, including, but not limited to existing socio-economic conditions. Examples include the use of hatcheries for egg protection and belief in the justice of payments for conservation outcomes. Direct payment schemes are considered ethical by members of communities where human population density and poverty are high. Our informants' adamant claims that offering alternative sources of income to replace the income lost from the collection and sale of eggs would not result in sea turtle egg protection in El Salvador are consistent with these results. Although our informants expressed a clear preference for direct payment for turtle eggs for protection, we are not suggesting that market forces somehow will guarantee the wellbeing of both hawksbills and *tortugueros* in El Salvador. *Tortugueros* sell sea turtles eggs at market value, just as commercial fishers sell fish at market value. The fact that some of the eggs are purchased by conservation organizations, as opposed to those wanting turtle eggs for consumption, does not guarantee that *tortugueros* are any more likely to employ sound conservation practices than commercial fishers whose livelihood also relies on the natural resource. What it does accomplish, however, is to alter *tortugueros*' position in the hawksbill conservation milieu. By selling turtle eggs to hatcheries for conservation, these local residents become

part of the conservation effort, which opens possibilities for acting on our final finding: the perceived need to include local residents in decision-making about hawksbill conservation policies.

The divergence between the priorities of international conservation experts and those of coastal residents in low-income regions can have serious implications for conservation and local community development. As Campbell (2007, p. 313) observes, "when these experts are active in policymaking at the international and national levels, and in designing conservation projects at the local level, their beliefs translate into material outcomes for local people living with sea turtles". International rejection of local residents as legitimate participants in conservation extends beyond hawksbills in El Salvador to any biodiversity conservation situation where human wellbeing is at stake. The approval or disapproval of a given practice by the international conservation community can essentially grant or deny its legitimacy in the eyes of international policymakers and funding organizations (Rodriguez et al., 2007).

Connecting International Priorities with Local Realities: Hawksbill Conservation in El Salvador

The three principal hawksbill nesting sites in El Salvador represent the largest known hawksbill nesting aggregation in the eastern Pacific Ocean (Gaos et al., 2010). With roughly 45% of all nesting activity in the region occurring in the Bahía (Fig. 1), it is a top priority for conservation interventions (Liles et al., 2011). These relatively high numbers of nesting hawksbills interspersed with coastal communities offer a unique

opportunity to integrate sustainable local development into an equally sustainable process of hawksbill recovery along the Salvadoran coast.

Sustainable sea turtle conservation requires integration of coastal communities into conservation initiatives (Nichols et al., 2000a). Despite the possibilities suggested by our informants and other critical social science research, however, experts within the international conservation community often limit the role of coastal communities to superficial levels, citing limited decision-making capacity as justification (Campbell 2000, 2002). Our research suggests the benefits of a fundamentally different approach, where *tortugueros* are recognized as key contributors in hawksbill research and conservation, whose direct participation in the development and implementation of project activities is critical to success.

To effectively link international conservation priorities with human wellbeing at the local level where most conservation occurs, conservationists must first understand primary resource users. Marginalized members of low-income regions collect millions of sea turtle eggs each year throughout the world, a number that can only be expected to rise as human numbers continue to increase in these regions. A myopic focus on the biological dimensions of sea turtle nest protection that dismisses the inherent social dimensions of conservation fails to address the livelihood needs of egg collectors, which are rooted in the specific contexts of individual nations and cultures. The international conservation community has the power and prestige to shape international policy and to determine funding priorities for sea turtle conservation activities. This can have seriously negative consequences for local conservation efforts that do not align with international

conservation priorities, particularly in low-income regions that require context-specific approaches to conservation that are informed by local realities. The divergence of international policy and funding priorities from local realities can dissuade local participation in conservation activities and construct a false dualism that fosters a perception of local egg collectors as the enemy of conservation and escalates latent conflict via direct competition for livelihood resources. In contrast, connecting international conservation policy and funding priorities to local realities, as has occurred with hawksbill conservation in El Salvador, enables all participants to build on existing synergies to garner local support for conservation that promotes joint-ownership in decision-making and active participation in all aspects of research and conservation. Ultimately, such synergies are required for sustainable, socially just conservation outcomes.

Our study of sea turtle conservation in low-income regions of El Salvador supports a growing body of evidence demonstrating that attempts to impose internationally negotiated uniform conservation strategies are failing in some cases where more locally shaped strategies have been more effective (Sayer and Collins 2012). Thus, understanding realities experienced by primary resource users is a prerequisite to analysis of the power structures operating in resource-based processes. Moreover, successfully aligning conservation strategies with local realities benefits wildlife and human wellbeing in both low- and high-income regions (Hutton and Leader-Williams 2003; Naughton-Treves et al., 2005; Robards and Lovecraft 2010). For all these reasons, conservation policies and practices must account for dynamic social contexts,

distributions of power, and interests of stakeholders—including primary resource users—to maximize the probability of their success.

CHAPTER III

ONE SIZE DOES NOT FIT ALL: IMPORTANCE OF ADJUSTING CONSERVATION PRACTICES FOR ENDANGERED HAWKSBILL TURTLES TO ADDRESS LOCAL NESTING HABITAT NEEDS IN THE EASTERN PACIFIC OCEAN*

OVERVIEW

Conservation biologists frequently use data from the same or related species collected in diverse geographic locations to guide interventions in situations where its applicability is uncertain. There are dangers inherent to this approach. The nesting habitats of critically endangered hawksbill sea turtles (*Eretmochelys imbricata*) cover a broad geographic global range. Based on data collected in the Caribbean and Indo-Pacific, conservationists assume hawksbills prefer open-coast beaches near coral reefs for nesting, and that individual hawksbills are highly consistent in nest placement, suggesting genetic factors partially account for variation in nest-site choice. We characterized nest-site preferences of hawksbills in El Salvador and Nicaragua, where >80% of nesting activity occurs for this species in the eastern Pacific, and ~90% of hawksbill clutches are relocated to hatcheries for protection. We found hawksbills

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*Reprinted with permission from "One size does not fit all: importance of adjusting conservation practices for endangered hawksbill turtles to address local nesting habitat needs in the eastern Pacific Ocean" by Liles, M.J., Peterson, M.J., Seminoff, J.A., Altamirano, E., Henríquez, A.V., Gaos, A.R., Gadea, V., Urteaga, J., Torres, P., Wallace, B.P., Peterson, T.R., 2015. Biological Conservation, 184, 405–413, Copyright 2015 by Elsevier Ltd.

preferred nest sites with abundant vegetation on dynamic beaches within mangrove estuaries. Nests in El Salvador were located closer to the ocean and to the woody vegetation border than nests in Nicaragua, suggesting female hawksbills exhibit local adaptations to differences in nesting habitat. Individual hawksbills consistently placed nests under high percentages of overstory vegetation, but were not consistent in nest placement related to woody vegetation borders. We suggest conservation biologists use caution when generalizing about endangered species that invest in specific life-history strategies (e.g., nesting) over broad ranges based on data collected in distant locations when addressing conservation issues.

INTRODUCTION

Conservation biology is grounded on awareness that practitioners attempting to conserve biodiversity and the long-term viability of natural systems often must act before being entirely confident in the sufficiency of available data (Soulé 1985, 1986). Subsequently, conservation scientists often adopt a precautionary approach and use data available from the same or related species compiled in distant geographic regions to help ground conservation practices in situations where its applicability is uncertain (Thompson et al., 2000; Gerrodette et al., 2002; Banks et al., 2010). There are dangers inherent to this approach, however, as the risks of precautionary management have been demonstrated for some broad-ranging species that exhibit variations in life-history strategies in heterogeneous environments across terrestrial (Smit et al., 2007), avian (Hansen and Urban 1992), and marine (Schofield et al., 2013) taxa. The inability of

precautionary management to address the local needs of certain targeted populations has led conservation biologists to increasingly implement evidence-based management (Pullin et al., 2004; Sutherland et al., 2004; Pullin and Knight 2009; Katselidis et al., 2013). Sea turtle species occur over broad portions of Earth, but detailed data are available for only a small subset of populations (National Research Council 2010; Wallace et al., 2011; Mazaris et al., 2014). This is particularly true concerning nesting behavior and factors underpinning nest-site selection (Hamann et al., 2010). Nest-site selection by egg-laying reptiles that lack postovipositional care, such as sea turtles, has important consequences for reproductive success. Biotic and abiotic factors— including predation (Leighton et al., 2011), substrate characteristics (Mortimer 1990), and temperature (Mrosovsky et al., 1984)—influence embryonic development of sea turtles (Wallace et al., 2004). Therefore, female turtles can influence hatchling survival (Wood and Bjorndal 2000), fitness (Mickelson and Downie 2010), and sex ratios (Mrosovsky et al., 1995) by selecting particular nest locations. Nest-site selection, however, may represent a trade-off between parental survival and the survival of offspring (Hughes and Brooks 2006; Katselidis et al., 2013). Nest placement near the high tide line increases the risk of embryo mortality by tidal overwash, but lowers the probability of depredation for hatchlings and females (Whitmore and Dutton 1985; Spencer 2002). Alternatively, greater distance from the high tide line may decrease the risk of inundation, but increases the susceptibility of eggs, hatchlings, and females to predation on the beach (Horrocks and Scott 1991). Therefore, nest sites are not always in what humans perceive as optimal locations.

Because many sea turtle populations are historically depleted, one common goal across sites is increasing hatchling production by relocating clutches of doomed eggs (i.e., clutches deposited in areas where mortality is imminent) to less vulnerable locations, such as hatcheries, to increase survival of hatchlings (Whitmore and Dutton 1985; Mrosovsky 2006). Despite the ubiquity of this practice, relocation of eggs to hatcheries often is criticized for altering biological processes and outcomes (Prichard 1980), including lowered hatching success (Boulon et al., 1996), biased sex ratios of hatchlings (Morreale et al., 1982), and decreased hatchling survival (Pilcher and Enderby 2001). Additionally, Mrosovsky (2006, 2008) contended that relocating doomed eggs might alter gene pools by selecting for turtles choosing vulnerable nest locations. For gene pools to be altered by doomed egg relocation, nest-site choice must be a heritable trait and differences in individual nest-site selection must be consistent (Pfaller et al., 2009). For instance, individual leatherback (*Dermochelys coriacea*) and loggerhead (*Caretta caretta*) turtles exhibit low repeatability (i.e., within-individual consistency) of nest-site selection, potentially due to their preference for oceanic nesting beaches with high wave energy that often are dynamic and unstable, suggesting that doomed egg relocation does not substantially distort the gene pool in these populations (Kamel and Mrosovsky 2004; Nordmoe et al., 2004; Pfaller et al., 2009). In contrast, Kamel and Mrosovsky (2005, 2006b) found high repeatability of nest-site selection by hawksbill turtles (*Eretmochelys imbricata*) along stable nesting beaches on Guadeloupe (Lesser Antilles), suggesting that some of the variability in nest-site preference arises from genetic factors, and that relocation of doomed eggs could distort gene pools

(Mrosovsky 2006).

Concerns about affecting gene pools via doomed egg relocation are particularly salient for hawksbills in the eastern Pacific. Fewer than 500 hawksbills nest along 15,000 km of coastline from Mexico to Peru, where >80% of known nesting activity is concentrated at Bahía de Jiquilisco in El Salvador and Estero Padre Ramos in Nicaragua (Gaos et al., 2010), and nearly 90% of hawksbill clutches at these 2 sites are relocated to hatcheries to prevent their consumption by humans (Altamirano et al., 2011; Liles et al., 2011). Contrary to their conspecifics in other oceanic regions that are coral reef dwellers with long-distance, offshore migrations (Meylan 1988; Miller et al., 1998), eastern Pacific hawksbills employ short, nearshore migrations between nesting and foraging areas in mangrove estuaries (Gaos et al., 2012). This marked difference in life history among hawksbill populations in distinct ocean basins underscores the need to characterize within-species or population-specific habitat use patterns to orient conservation strategies for highly endangered species that occur widely across the globe. Despite the relative abundance of life history data available for hawksbills in the Atlantic (e.g., Bjorndal et al., 1985; Meylan 1999) and the Indo-Pacific (e.g., Loop et al., 1995; Mortimer and Donnelly 2008), little information exists for hawksbills in the eastern Pacific, particularly on nesting ecology, which may impede efforts targeting their recovery.

For these reasons, we investigated nest-site selection by hawksbills in the eastern Pacific to provide a more comprehensive understanding of regional variation in this species and to elucidate the potential consequences of doomed egg relocation in this

region. Specifically, we characterized the microhabitat preferences and repeatability of nest-site choice by hawksbills in Bahía de Jiquilisco in El Salvador and Estero Padre Ramos in Nicaragua. Our results provide the first assessment of nest-site selection by individuals of this severely depleted hawksbill population and offer insight into priority areas for conservation. Based on our findings, we clarify the implications of doomed egg relocation programs on gene pools of hawksbills in El Salvador and Nicaragua and discuss potential negative consequences of generalizing about endangered species that invest in specific life-history strategies, such as nest-site choice, across broad geographic ranges.

METHODS

Study Sites

Our study areas were situated within the mangrove estuary complexes of Bahía de Jiquilisco (13°130 N, 88°320 W) in El Salvador and Estero Padre Ramos (12°480 N, 87°280 W) in Nicaragua, which flank the western and eastern sides of Gulf of Fonseca on the Pacific coast of Central America, respectively (Fig. 2). Inshore sandy beaches (54.9 km) within mangrove estuaries at these two study areas host >80% of known hawksbill nesting activity in the eastern Pacific (Gaos et al., 2010; Altamirano et al., 2011; Liles et al., 2011). Hawksbill nesting occurs primarily between May and October, with a peak June–July. High poverty levels are common to both areas, with most households lacking potable water and waste collection services, discontinuing education at middle school level, and earning USD$162 per month (ICAPO 2012). The

exploitation of wild natural resources, such as fishing, mollusk extraction, and sea turtle egg collection, is an important source of income for impoverished residents of Bahía de Jiquilsico and Estero Padre Ramos. Human consumption of sea turtle eggs is illegal in both countries (República de Nicaragua 2005; República de El Salvador 2009), but limited enforcement by authorities, scarce employment options, and high-density human populations located near hawksbill nesting beaches result in the collection of nearly 100% of eggs by local residents in Bahía de Jiquilisco and Estero Padre Ramos. This renders protection of hawksbill nests in situ infeasible on most beaches. Consequently, conservation organizations implement hatcheries and purchase hawksbill eggs collected by local residents, which provides an alternate economic incentive to sale for human consumption. This approach has gained acceptance among coastal communities as a socially just conservation strategy; eggs not purchased by conservation organizations are sold illegally for human consumption on local markets (Liles et al., 2014).

Bahía de Jiquilisco is located in the Department of Usulután on the south-central coast of El Salvador and is a National Conservation Area, RAMSAR wetland, and UNESCO Biosphere Reserve (MARN 2013a). It is the largest mangrove forest in El Salvador (635 km^2), and includes numerous estuaries, channels, and islands. Bahía de Jiquilisco has 42.1 km of hawksbill nesting habitat composed of a series of 8 discernible fine-grained sand beaches with 3 hatcheries and 1 in situ nest protection area (Fig. 2). Open sand beaches are narrow, ranging from 0 to 12 m in width, with a mosaic of secondary coastal forest (e.g., mesquite [*Prosopis juliflora*], Madras thorn [*Pithecellobium dulce*], buttonwood [*Conocarpus erectus*]), and small-scale plantations

of fruit trees (e.g., coconut palm [*Cocos nucifera*], tallow wood [*Ximenia americana*], cashew [*Anacardium occidentale*]) reaching the high tide line in most areas.

Estero Padre Ramos is located in the Department of Chinandega on the northwestern Pacific coast of Nicaragua. Declared a Nature Reserve in 1983, it covers 88 km^2 (MARENA 2003), of which 26 km^2 are mangrove forest (Carvalho et al., 1999). Estero Padre Ramos consists of a large estuary, extensive lagoons, and 8 distinct fine-grained sand beaches totaling 12.8 km, with 1 hatchery and 1 in situ nest protection area (Fig. 2). Open sand beach widths vary between 0 and 8 m, and are backed by intact second-growth coastal forest (e.g., mesquite, Madras thorn, Güiligüiste [*Karwinskia calderoni*]) often extending to the high tide line.

Nest Sampling

Nest sampling occurred from 1 May to 15 October 2011–2013 in Bahía de Jiquilisco and 1 May to 15 October 2012–2013 in Estero Padre Ramos. Project personnel and an extensive network of >200 trained local egg collectors patrolled nesting habitat from 18:00 to 06:00 daily by foot and boat in search of female hawksbills. We identified turtles by Inconel tags (National Brand & Tag, Newport, KY, USA) located on the second proximal scale at the edge of both front flippers and internal passive integrated transponders (PIT tags; Biomark, Boise, ID, USA) in the right front flipper; Inconel and PIT tags were either present from application during previous tagging seasons or were applied after egg laying had finished. Because of the temporally dispersed (e.g., 1–5 nests per night) and low-density nesting by hawksbills at both sites

(e.g., 1 nest per 2 km), logistical and economic limitations prevented us from identifying all nesting turtles and sampling all nest sites.

Measurements

For each female hawksbill encountered, we measured curved carapace length (nuchal notch to posterior-most tip of marginal scutes) after egg laying had completed to avoid disturbance during nesting. To determine patterns in nest-site selection, we first measured the distance from the egg chamber to the current high water line (maximum water height at time of egg laying). Unlike the study area of Kamel and Mrosovsky (2005, 2006b), which presented an unbroken forest line over the entire site, the forest line along the beaches of Bahía de Jiquilisco and Estero Padre Ramos is irregular or fragmented into patches of littoral vegetation. We therefore measured the distance from the egg chamber to the woody vegetation border, defined as the point where the forest or plantations of fruit trees began. We concluded nest site measurements by estimating the overstory vegetation cover, defined as the percent cover directly above the nest measured with a convex spherical densitometer (Ben Meadows, Janesville, WI, USA). The location of each nest was georeferenced using a handheld Global Positioning System (GPS) receiver (eTrex, Garmin International, Olathe, KS, USA). We assigned each nest site to 1 of 4 beach zones, from ocean-to-forest, based on vegetative cover: (1) open sand (no vegetation), (2) non-woody vegetation (presence of herbaceous vegetation), (3) woody vegetation border (near the forest or plantations, but not completely surrounded by trees), and (4) woody vegetation (surrounded by trees).

Data Analyses

We formulated competing nominal logistic regression models using each of 5 variables (distance to current high water line, distance to woody vegetation border, percentage of overstory vegetation cover, site and year) singly, in pairs, collectively, and with interactions to explain beach zone selection by female hawksbills for all nests. Because female turtles were not observed at all nesting events, we assessed identical candidate models, with the addition of curved carapace length, using the subset of the data that included only nests with measured females. This approach allowed us to evaluate the importance of female size in nest-site selection, while using data from all nests when exploring the roles of the 5 nest-placement variables. We compared models within an information-theoretic approach to model selection using Akaike's information criterion corrected for small sample size (AIC_c), and calculating the associated Akaike weights (w_i) for each model (Burnham and Anderson 2002). We evaluated model performance by calculating the area-under-the-curve (AUC) of the receiver operating characteristics (ROC) plot (Field and Bell 1997), and considered AUC values of 0.5–0.7, 0.7–0.8, 0.8–0.9, and >0.9 as poor, acceptable, excellent, and outstanding agreement between predictions and observations, respectively (Swets 1988; Hosmer and Lemeshow 2000).

To quantify individual differences in nest-site selection, we calculated the repeatability (r) of nest-site choice by female hawksbills that deposited $\geq$2 clutches per year during 2011–2013 using the methods described by Lessells and Boag (1987). We

computed all analyses using JMP Pro 11.0.0 (SAS Institute, Cary, NC, USA), with an alpha level of 0.05 where relevant.

RESULTS

We measured the position of 694 nests (76% of total nests) from a minimum of 188 individual hawksbills in 2011 through 2013, representing nearly 40% of total mature female hawksbills estimated to exist in the eastern Pacific (Gaos et al., 2010). Of these nests, 405 (58%) were recorded in Bahía de Jiquilisco and 289 (42%) in Estero Padre Ramos. The mean size of the 694 clutches was 160.7 eggs (SE 1.35, range = 45–253), with significantly larger clutches deposited in Bahía de Jiquilisco (167.8 eggs, SE 1.68, n = 405) than in Estero Padre Ramos (150.6 eggs, SE 2.08, n = 289; t = 7.24, df = 692, P < 0.0001). When selecting nest sites, turtles demonstrated a marked preference for the woody vegetation border and woody vegetation (98.3%, n = 682), with only 1 nest placed in open sand (Fig. 3). In Bahía de Jiquilisco, turtles placed most nests in the woody vegetation border (54.1%, n = 219), whereas turtles in Estero Padre Ramos selected locations primarily in woody vegetation (79.9%, n = 231). The mean distance from the nest to the high water line across both sites was −11.9 m (SE 0.71, n = 694), with nests located closer to the water in Bahía de Jiquilisco (−8.5 m, SE 0.58, n = 405) than in Estero Padre Ramos (−14.5 m, SE 1.14, n = 289; negative values indicate landward distance from water line). Nests were likewise placed nearer the woody vegetation border in Bahía de Jiquilisco (−5.1 m, SE 0.41) than in Estero Padre Ramos (−10.7 m, SE 0.76; overall −8.3 m, SE 0.49). Overall, turtles preferred nest sites with

abundant overstory vegetation cover (88.8%, SE 0.86), with an average of 84.1% (SE 1.03) in Bahía de Jiquilisco and 92.5% (SE 1.23) in Estero Padre Ramos.

The best-approximating model for predicting beach zone selection by female hawksbills using the complete data set (n = 694 nests) included all 5 predictor variables (w_i = 0.793), which had nearly 6 and 14 times the empirical support as the second- and third-ranked models, respectively (Table 2). The top 3 models constituted the 95% confidence set and were plausible, with a cumulative $\Delta AIC_c < 7$ (Burnham et al., 2011). AUC values for these models ranged from 0.81 to 1.00, indicating excellent model performance. Woody vegetation border and year were the most strongly supported predictor variables and appeared in the 5 best-approximating models, whereas site appeared in the top 4 models.

The 188 measured female turtles had an overall mean carapace length of 82.6 cm (SE 0.43, range = 68–98), with significantly larger turtles nesting in Bahía de Jiquilisco (84.7 cm, SE 0.57, n = 86) than in Estero Padre Ramos (81.3 cm, SE 0.59, n = 102; t = −4.13, df = 186, $P < 0.0001$). For the subset of nesting data that included measured female turtles (n = 387 nests), the best-supported model that included carapace length was the lowest-ranked plausible model in the 95% confidence set (w_i = 0.014), and was 26 times less likely than the best-approximating model (w_i = 0.375) for predicting beach zone selection by female hawksbills (Table 3). The 3 models that constituted the 95% confidence set for the complete data set (n = 694 nests) were also included in the 95% confidence set using the subset of data. Woody vegetation border and year were likewise the most strongly supported predictor variables and appeared in the 6 best-approximating

models.

For the 694 total nests observed, we identified 123 individual turtles that nested ≥2 times per year (2–5 clutches/turtle, n = 330 nests) and 65 individuals that nested 1 time (the female turtle was not identified for 299 nests). Turtles that deposited ≥2 clutches in Estero Padre Ramos had significant repeatability of nest-site choice in relation to the current high water line (r = 0.34, n = 66 turtles and 185 nests, $P < 0.0001$), whereas females in Bahía de Jiquilisco were inconsistent (r = 0.07, n = 57 turtles and 145 nests, P = 0.2250; Fig. 4a). Turtles did not demonstrate repeatability in nest placement with respect to the woody vegetation border at either site (Bahía de Jiquilisco, $r = -0.10$, P = 0.8483; Estero Padre Ramos, r = 0.11, P = 0.0796; Fig. 4b), but exhibited significant consistency in their preference of percent overstory vegetation cover at both sites (Bahía de Jiquilisco, r = 0.62, $P < 0.0001$; Estero Padre Ramos, r = 0.68, $P <$ 0.0001; Fig. 4c).

DISCUSSION

Our data on the nesting ecology of hawksbills in the eastern Pacific contrast with the prevailing paradigm of hawksbills being coral reef-dwellers that use stable open-coast beaches for nesting (e.g., Loop et al., 1995; McClenachan et al., 2006; Mrosovsky 2006). Female hawksbills in Bahía de Jiquilisco in El Salvador and Estero Padre Ramos in Nicaragua primarily selected nest sites on dynamic beaches within mangrove estuaries. This life-history strategy, coupled with their use of mangrove estuaries for foraging (Gaos et al., 2012), explains—at least in part—why mature female hawksbills

went virtually undetected in the eastern Pacific until recently and why recovery efforts targeting the species were limited and largely ineffective (e.g., NMFS and USFWS 1998).

Hawksbills in Bahía de Jiquilisco and Estero Padre Ramos manifested a strong preference for nest sites with woody vegetation (98.3%) and abundant overstory vegetation cover (mean of 88.8%). Model-selection supported this finding, with the predictor variables woody vegetation border and overstory vegetation cover represented in 5 and 3 of the 5 best-approximating models, respectively (Table 2). Hawksbills rarely placed nests in open sand or non-woody vegetation (Fig. 3), which underscores the critical importance of woody vegetation for the nesting success of hawksbills in the eastern Pacific. These results differ from studies conducted in the Caribbean and Indo-Pacific, where hawksbills placed higher percentages of nests in open sand (e.g., 46.4%, Bjorndal and Bolten 1992; 22.0%, Loop et al. 1995; 6.0%, Kamel & Delcroix 2009) and non-woody vegetation (e.g., 10.8%, Loop et al., 1995; 33.3%, Kamel and Mrosovsky, 2005; 31.8%, Kamel and Delcroix, 2009) with lower percentages of overstory vegetation cover above nests (e.g., 32.8%, Kamel and Mrosovsky 2005). Additionally, several studies in distant ocean basins demonstrated that individuals across all species of sea turtles, including hawksbills, tended to nest at a mean elevation of ~1 m above sea level, irrespective of overstory vegetation cover and distance from the high water line—gentle slopes resulted in a wider range of nest distributions and steeper slopes resulted in nests located predominantly closer to the ocean (Johannes and Rimmer 1984; Horrocks and Scott 1991; Wood and Bjorndal 2000; Weishampel et al., 2003; Katselidis et al., 2013).

Other studies, however, showed that sea turtles in certain regions preferred nest sites at higher elevations (Fish et al., 2005; Fuentes et al., 2010), which highlights potential behavioral plasticity within species. Although we did not measure nest elevation, the nesting beaches at our study areas are low relief with minimal elevation change and, therefore, elevation is likely not as useful an environmental cue for hawksbills nesting in mangrove estuaries as for sea turtles nesting on open-coast beaches with steeper profiles. For example, most nesting beaches in Bahía de Jiquilisco have a gentle slope that reaches an elevation of $\leq$1 m across their entire width ($\leq$50 m), yet nest placement by hawksbills is highly concentrated at ~8.5 m from the high water line (Fig. 4a), suggesting that other factors, such as proximity to beach vegetation, are more informative in explaining the distribution of nests. We suspect these differences reflect biophysical conditions of our study sites, including the near absence of non-woody vegetation, the extension of woody vegetation to the high water line at most beaches, and the low relative elevation of nesting beaches above sea level. Similar variation in the selection of nest site locations exists for other sea turtle species, as exemplified by loggerheads that primarily nest near or above the vegetation line on exposed tidal beaches in Florida, USA (Hays et al., 1995) and below the vegetation line on minimally tidal beaches in the Mediterranean (Katselidis et al., 2013). These disparities further emphasize the need for evidence-based approaches to conservation management of sea turtles and species with similar life histories.

Despite the overall preference of hawksbills for nest sites with woody vegetation and abundant overstory cover, the location of nests differed between sites, which

suggests that female hawksbills exhibited local adaptations to differences in nesting habitat. For example, only a narrow tract of secondary forest measuring 10–15 m wide adjacent to the high water line is present at most beaches in Bahía de Jiquilisco, whereas intact second-growth forest extends >100 m landward from the high water line at most beaches in Estero Padre Ramos (Fig. 5). Nest placement by hawksbills at both sites reflected this difference in availability of suitable habitat, with nests in Bahía de Jiquilisco restricted to just over half the distance to the current high water line (Fig. 4a) and to less than half the distance to the woody vegetation border (Fig. 4b) as nests in Estero Padre Ramos. Additionally, hawksbills placed >50% of nests in the woody vegetation border in Bahía de Jiquilisco and nearly 80% of nests in woody vegetation in Estero Padre Ramos (Fig. 3), which may be attributed to the fragmented state of woody vegetation at nesting beaches in Bahía de Jiquilisco relative to those available to hawksbills in Estero Padre Ramos. Our results revealed a similar difference in the percentage of overstory vegetation cover above nests—with 84.1% and 92.5% in Bahía de Jiquilisco and Estero Padre Ramos, respectively—further accentuating the degraded condition of available woody vegetation in Bahía de Jiquilisco. Based on these data, we suggest that the Government of El Salvador adopt protective measures for beaches similar to those currently existing in Nicaragua. There, the initial 100 m landward from the maximum high tide line are classified as core protected areas where human use is prohibited. Human use also is prohibited in the next 100 m landward unless governmental permission is obtained (República de Nicaragua 2009). Because hawksbills placed their nests as far as 85 m inland from the high water line, such

legislation would facilitate permanent availability of intact woody vegetation at these critical nesting beaches.

Individual female hawksbills that nested $\geq$2 times per year demonstrated significant repeatability of nest-site choice in relation to the percentage of overstory vegetation cover above nests at both sites (Fig. 4c). These values were similar to those reported for hawksbills in the Caribbean ($r = 0.71$, Kamel & Mrosovsky 2005; $r = 0.69$, Kamel and Mrosovsky 2006b). Turtles were inconsistent, however, in their nest placement with regard to woody vegetation border at both sites and did not demonstrate repeatability of nest-site selection with respect to the current high water line in Bahía de Jiquilisco, which contrasts with nesting behavior described for hawksbills in the Caribbean (Kamel and Mrosovsky 2005, 2006b). The difference in nest-site consistency is likely a consequence of the need for female hawksbills to navigate environmental stochasticity induced by the unstable and dynamic nature of nesting beaches within mangrove estuaries. The instability of nesting beaches is further intensified in Bahía de Jiquilisco by continued degradation of supralittoral and littoral vegetation, which stimulates events of severe erosion and accretion annually. Given the potential variability of nesting habitat between sites among years, it is not surprising that all plausible models using the complete data set included the variables site and year as important predictors of beach zone selection by female hawksbills (Table 2).

Our results have important implications for the relocation of doomed hawksbill eggs in the eastern Pacific, where conservationists relocate nearly 90% of hawksbill clutches from Bahía de Jiquilisco and Estero Padre Ramos to hatcheries so they are not

consumed by humans. Because relocation of eggs from individual turtles that consistently place nests in vulnerable areas may distort gene pools (Pfaller et al., 2009), some biologists have questioned the validity of doomed egg relocation as a conservation strategy (Mrosovsky 2006, 2008). Our findings, however, indicate that individual hawksbills were not consistent regarding nest placement with respect to the woody vegetation border in Bahía de Jiquilisco and Estero Padre Ramos (Fig. 4b). The significance of site and year also suggests that nest-site selection patterns are highly variable in space and time. Additionally, individual hawksbills frequently selected nest sites on distinct beaches within and among years at both sites. Taken together, the low repeatability values we documented suggest that high stochasticity in nesting habitat available to eastern Pacific hawksbills may be selecting for a greater degree of heritable behavioral plasticity in nest-site choice. Therefore, nest relocation should not be detrimental to the gene pool of hawksbills in the eastern Pacific, and could continue to be used as a tool to increase hatchling production and enhance population recovery. This finding does not imply, however, that nest relocation does not affect the sex ratios of hatchlings. Because turtles exhibit temperature dependent sex determination, nests placed under vegetation or near the ocean reduce sand temperature and increase the production of male hatchlings (Katselidis et al., 2012; Wood et al., 2014). Thus, nest relocation could affect offspring sex ratios if the sites of relocation did not reflect the shading or sand moisture conditions of the original site of deposition.

Our findings demonstrate marked within-species disparities among hawksbill life-history characteristics among ocean regions and provide insight into the potential

consequences of relying on data collected from hawksbills in the Caribbean and Indo-Pacific to guide conservation for eastern Pacific hawksbills. Because habitat protection is an essential component of conservation, safeguarding critical nesting areas is paramount to the survival of endangered species. Utilizing precautionary management practices in the eastern Pacific centered on the widely accepted assumption that hawksbills prefer open-coast beaches near coral reefs for nesting would perpetuate ineffective recovery efforts. Instead, conservationists can employ our results to effectively target primary nesting beaches in mangrove estuaries and formulate evidence-based conservation actions that are aligned with microhabitat preferences of eastern Pacific hawksbills. Similarly, using data from the Caribbean that indicate individual hawksbills are consistent nesters to inform egg protection strategies in the eastern Pacific would be misguided considering our contrasting results. Anthropogenic pressures in El Salvador and Nicaragua require hawksbill conservation programs to relocate clutches to hatcheries so eggs will not be consumed by people (Altamirano et al., 2011; Liles et al., 2011). Moreover, because hatchery operations are driven by slowly-formed social processes that emerged from local realities of impoverished coastal communities, local conservation support is required; altering hatchery-oriented methods of nest protection could spark conflict and diminish conservation outcomes (Liles et al., 2014). Future studies addressing nest-site selection by eastern Pacific hawksbills should determine how vegetation characteristics (e.g., patch size and composition), geomorphic attributes (e.g., physical landmarks and bathymetry), and human disturbances of beaches influence nest-site choice at larger spatial scales. Additionally, future research should

estimate the amount of available nesting habitat and assess habitat quality using demographic or physiological indicators from hatchling hawksbills, such as body condition and primary sex ratios, which can give insight into conditions of the terrestrial environment at nest sites where embryos develop. Such studies would provide invaluable information to further guide locally tailored conservation strategies.

Our study demonstrates that hawksbill sea turtles in the eastern Pacific select heavily vegetated nest sites on dynamic beaches in mangrove estuaries, which contrasts with the nesting behavior of this species in other ocean basins. Female hawksbills exhibit local adaptations in nest placement to differences in nesting habitat and require that conservation efforts be tailored to local conditions for effective recovery. Interventions that assume homogeneity of species or systems across vast geographic locations could have serious negative consequences for species or systems that exhibit heterogeneity across their range, particularly for populations of highly endangered species, such as hawksbill sea turtles. Our findings support the growing body of literature that highlights the value of evidence-based as opposed to precautionary conservation management and underscores the importance of conservation biologists using care when generalizing about endangered species with broad ranges of certain life-history strategies based on data collected from small-scale studies conducted in distant locations.

CHAPTER IV

POTENTIAL LIMITATIONS OF BEHAVIORAL PLASTICITY IN AN ENDANGERED SPECIES AND THE ROLE OF EGG RELOCATION IN CLIMATE CHANGE ADAPTATION

OVERVIEW

Anthropogenic climate change is widely considered a major threat to global biodiversity and the ability of a species to develop compensatory responses to climate-driven environmental change will determine its likelihood of survival. Hawksbill sea turtles (*Eretmochelys imbricata*) are critically endangered species that exhibit temperature-dependent sex determination, where nest temperatures determine the sex of offspring. The objectives of our study were to generate thermal profiles of nest environments and estimate sex ratios and physical condition of hatchling hawksbills under natural and artificial conditions at Bahía de Jiquilisco, El Salvador and Estero Padre Ramos, Nicaragua, to learn whether behavioral plasticity in this species is likely to compensate for projected climate change and what the role of egg relocation may be as an adaptation strategy. We found that the woody vegetation (i.e., coastal forest and small-scale plantations of fruit trees) zone produced the lowest temperatures of all monitored zones, but that there were only minimal differences in temperature between sand depths. Additionally, we found that in situ clutches at both sites currently incubate at higher temperatures, obtain a lower hatching success, produce a higher percentage of female hatchlings, and produce smaller hatchlings than clutches relocated to hatcheries.

Our findings suggest that adjustment of nest depth by hawksbills is unlikely to compensate for climate change in mangrove estuaries and we contend that egg relocation can contribute significantly to recovery efforts under appropriate circumstances.

INTRODUCTION

Anthropogenic climate change is widely considered a major threat to global biodiversity (Parmesan and Yohe 2003; Foden et al., 2013), with 15–37% of Earth's species potentially 'committed to extinction' by 2050 (Thomas et al., 2004). The ability of a species to develop compensatory responses to climate-driven environmental change will determine its likelihood of survival; species that adjust to new environments or adapt to local climatic conditions will persist while those that fail to adjust or adapt will not (Sinervo et al., 2010). Because the impacts of climate change can vary among taxa and geographic regions (Parmesan 2007), species employ diverse adaptive responses—including spatial shifts in range (e.g., Chen et al., 2011) and temporal shifts in behavior (e.g., Yang and Rudolf 2010)—to mitigate unfavorable conditions (Bellard et al., 2012).

There is growing concern, however, that life histories of some species may predispose them to higher levels of vulnerability than other species (Duputié et al., 2015). For example, ectotherms are particularly sensitive to changes in thermal regimes (Telemeco et al., 2009). In most reptiles, nest temperature regulates egg incubation, determines offspring sex, and affects progeny performance (e.g., Bull 1980; van Damme et al., 1992; Georges 2013). Females could respond to climate change by altering aspects

of nest-site choice that include nesting phenology (i.e., timing of nesting), location of nest (e.g., amount of shade cover), and nest depth (Ewert et al., 2005; Schwanz and Janzen 2008; Refsnider et al., 2013). Doody et al., (2006), for example, found that maternal nest-site choice compensated for climatic variation among populations of the Australian water dragon (*Physignathus lesueurii*). Similarly, Refsnider and Janzen (2012) determined that behavioral plasticity in painted turtles (*Chrysemys picta bellii*) allowed females to match shade cover over nests with prevailing environmental conditions to influence the sex ratio of offspring.

Sea turtles are long-lived, late-maturing species that exhibit temperature-dependent sex determination (TSD). Given their complex life histories and reliance on marine and terrestrial habitats during their lifecycle, it is unclear how sea turtles will respond to climate-driven change in these environments. Changes in nesting phenology of sea turtles are increasingly observed worldwide (e.g., Weishampel et al., 2010; Dalleau et al., 2012; Neeman et al., 2015) and further shifts in the global distribution of nesting are forecasted (Pike 2013a, b). Additionally, because TSD and thermal thresholds of embryonic development are highly conserved among sea turtle species (Ackerman 1997; Davenport 1997; Wibbels 2003), female turtles could alter nest depth to mitigate changes in temperature (Roosenburg 1996). Regardless, whether behavioral plasticity in nesting will enable sea turtles to persist within their climatic niche remains uncertain (Hawkes et al., 2007; Hamann et al., 2010).

Successful egg development in sea turtles must occur between 25 and 35^{o}C (Ackerman 1997), and temperature variations of ~1^{o}C can markedly skew hatchling sex

ratios (Mrosovsky et al., 2009). Most studies report female-biased sex ratios (Wibbels 2003; Hawkes et al., 2009), with some highly skewed populations currently producing ≥90% female offspring (Marcovaldi et al., 1997; Godfrey et al., 1999; Broderick et al., 2000; Patino-Martinez et al., 2012b; Marcovaldi et al., 2014). Climate models predict levels of warming between +1.6 and +4.0^{o}C for Central America by 2100 (Magrin et al., 2014), which would place additional thermal stress on embryonic development that already may be nearing lethal thresholds in many populations (Valverde et al., 2010; Santidrán Tomillo et al., 2012; Pike 2014).

Given the potential limitations of plastic compensatory responses of sea turtles to accelerated changes in thermal conditions of nesting beaches, it is possible that sea turtles will be unable to adapt quickly enough to offset negative consequences to population demographics and human intervention may be required. The relocation of sea turtle eggs as a management strategy used to increase hatchling production and enhance population recovery is ubiquitous worldwide (Naro-Maciel et al., 1999; Formia et al., 2003; Garcia et al., 2003; Chacon-Chaverri and Eckert 2007; Patino-Martinez et al., 2012a), but often is criticized for conceivably altering biological processes and outcomes (Prichard 1980; Pilcher and Enderby 2001; Mrosovsky 2006). By utilizing internationally-recognized best practices (Eckert et al., 1999) throughout the egg relocation process, however, many of the undesired biological outcomes can be avoided or mitigated (Marcovaldi and Marcovaldi 1999a; Kornaraki et al., 2006; Patino-Martinez et al., 2012b). Because temperatures are predicted to increase substantively in Central America over a relatively short period, better data regarding the influence of sea turtle

egg relocation on the thermal regimes of nest environments, primary sex ratios, and hatchling condition—and how those results compare with data collected from in situ nests—is essential, particularly for severely depleted populations of highly endangered species.

We addressed these needs by focusing our study on critically endangered hawksbill sea turtles (*Eretmochelys imbricata*) in the eastern Pacific Ocean. This population is among the most threatened (Wallace et al., 2011) and least resilient (Fuentes et al., 2013) sea turtle populations in the world, with fewer than 500 adult females nesting along 15,000 km of Latin American coastline (Gaos et al. 2010). Further, >80% of this nesting activity is concentrated on low-relief beaches in mangrove estuaries at Bahía de Jiquilisco, El Salvador, and Estero Padre Ramos, Nicaragua (Altamirano et al., 2011; Liles et al., 2011; Liles et al., 2015)—ecosystems that are particularly vulnerable to increasing global temperatures (Gilman et al., 2008).

The objectives of our study were to generate thermal profiles of nest environments and estimate sex ratios and physical condition of hatchling hawksbills under natural and artificial conditions to learn whether behavioral plasticity in this species is likely to compensate for projected climate change and what the role of egg relocation may be as a mitigation strategy. To achieve these objectives, we (i) generated and analyzed thermal profiles of a high-density nesting beach, deforested areas, and hatcheries at Bahía de Jiquilisco, El Salvador; and (ii) evaluated differences in the thermal characteristics of the nest environment, offspring sex ratios, and hatchling condition at Bahía de Jiquilisco and Estero Padre Ramos, Nicaragua, across three nest

protection strategies (i.e., in situ, translocated on beach, and relocated to hatcheries). Our results provide the first empirical assessment of nest protection strategies for this severely depleted population in the eastern Pacific Ocean. Based on our findings, we offer recommendations for mitigation strategies that complement the plastic adaptive responses to climate change demonstrated by nesting hawksbills in mangrove ecosystems.

METHODS

Our study was conducted at Bahía de Jiquilisco (13°13°N, 88°32°W) in El Salvador and Estero Padre Ramos (12°48°N, 87°28W) in Nicaragua, which are located on the western and eastern borders of Gulf of Fonseca on the Pacific coast of Central America, respectively (Fig. 6). Hawksbill nesting occurs primarily between May and September, with a peak in June and July, along sandy beaches (54.9 km) in mangrove estuaries at these two sites.

Bahía de Jiquilisco is located on the south-central coast of El Salvador and has hawksbill nesting habitat (42.1 km) comprised of eight distinct fine-grained sand beaches with three hatcheries and one in situ nest protection area (Fig. 6). A fragmented mosaic of second-growth coastal forest and small-scale fruit trees plantations measuring 10–15 m wide adjacent to the high water line is present at most beaches (Liles et al., 2015). Moderate development exists in some nesting areas, particularly along eastern and western Punta San Juan, eastern and western Isla Madresal, and northern Isla San Sebastian. Estero Padre Ramos is situated on the northwestern Pacific coast of Nicaragua

and consists of eight discernable fine-grained sand beaches (12.8 km), with one hatchery and one in situ nest protection area (Fig. 6). Intact secondary coastal forest extends >100 m landward from the high water line at most beaches (Liles et al., 2015). Nesting areas have experienced minimal development, with Padre Ramos most impacted.

Nesting Frequency and Nest Protection Strategies

Beach patrols occurred from 1 April to 15 October 2011–2013 at Bahía de Jiquilisco and 1 May to 15 October 2010–2013 at Estero Padre Ramos, where project personnel and a network of >200 trained local egg collectors monitored nesting habitat from 18:00 to 06:00 daily by foot and boat in search of female hawksbills and nests. Because of the depressed socioeconomic conditions of coastal communities in both countries, local residents consider hawksbill eggs an economic resource, resulting in the collection of nearly 100% of eggs (Liles et al., 2014). Consequently, conservation organizations purchase the eggs encountered and/or collected by local residents for protection to prevent their sale for human consumption. Each nesting season ~10% of hawksbills clutches typically are protected in situ via agreements with local residents to not collect the eggs, and ~90% of clutches are translocated to nearby areas of the beach or relocated to hatcheries to avoid human depredation.

The protection strategy employed for encountered nests depended on their location and the year at each site. At Bahía de Jiquilisco during 2011–2013, clutches deposited at the in situ protection area along Las Isletas beach were not manipulated; however, we buried a surface-enclosed wire mesh cylinder (diameter, 50 cm; height, 60

cm) around each clutch at a depth of ~55 cm after oviposition had completed to avoid predation of eggs; we removed this barrier three days prior to the estimated date of hatching or when a depression in the sand was observed. Clutches deposited at beaches ≤3 km from the in situ protection area were translocated to Las Isletas beach for protection, except in 2013, when clutches were relocated to a hatchery. We relocated remaining clutches to a hatchery at Isla San Sebastian or a hatchery at Punta San Juan, depending on the location of deposition. In Estero Padre Ramos during 2010–2013, we did not manipulate clutches deposited at the in situ protection area at La Tigra beach. We relocated all clutches deposited at other beaches to a hatchery at Punta Venecia, except in 2010 and 2011, when some clutches were translocated to an area of beach at Punta Venecia when the hatchery reached capacity and when the hatchery was not yet operational, respectively.

For clutches relocated to the hatchery or translocated on the beach, we measured the dimensions of original nest cavities and attempted to emulate them in artificial nests. However, at Estero Padre Ramos during 2010–2011, artificial nests often were deeper than the original nest cavities. We relocated most clutches ≤12 h after deposition to minimize movement-induced mortality during transfer and reburial. For clutches relocated to a hatchery or translocated on the beach at Bahía de Jiquilisco, we measured the transport time (length of time between egg deposition by the turtle and reburial in the artificial nest) of each clutch.

Thermal Profiles of Sand and Nests

To measure intrabeach variation in temperature during the hawksbill nesting season, we buried HOBO U22 data loggers (Water Temp Pro v2, Onset Computer Corporation, Bourne, MA, USA; n = 28) in four beach zones at two sand depths (30 and 60 cm) along three transects, each separated by 500 m (Kamel and Mrosovsky 2006a), at Las Isletas beach in Bahía de Jiqulisco during 2012–2013. Beach zones were assigned from ocean-to-forest, based on vegetative cover: (i) open sand (no vegetation), (ii) non-woody vegetation (herbaceous vegetation), (iii) woody vegetation border (near the forest or plantations, but not completely surrounded by trees), and (iv) woody vegetation (surrounded by trees) (Liles et al., 2015). We also placed data loggers (n = 12) in areas cleared of vegetation to more accurately assess the effects of deforestation on thermal conditions of nesting beaches (Kamel and Mrosovsky 2006a). Data loggers had a resolution of 0.02^{o}C with an accuracy of $\pm$0.2^{o}C, and recorded the temperature every 30 min. We averaged recorded values to give a mean daily temperature for each logger. Data loggers that were not recovered (n = 3) or did not function properly during data collection (n = 1) were excluded from analyses.

To protect hawksbill clutches deposited on beaches where in situ protection and translocation were infeasible, shaded hatcheries were constructed at nesting beaches at both sites that typically operated from 1 May to 31 October annually and whose dimensions varied according to the capacity required for relocated clutches (Table 4). At Bahía de Jiquilisco from 2012 through 2013, we buried data loggers (n = 10) in the center of each hatchery at two sand depths (30 and 60 cm). The temperature was

recorded every 30 min and then averaged to obtain a mean daily temperature for each logger. Data loggers that malfunctioned during data collection (n = 3) were not included in analyses. To measure the temperature in hawksbill nests during the incubation period, we placed HOBO U22 or HOBO U23 (Pro v2 Temperature/Relative Humidity, Onset Computer Corporation, Bourne, MA, USA) data loggers in the center of the egg mass of clutches incubated in situ, translocated on the beach, and in hatcheries at Bahía de Jiquilisco during 2011–2013 and in Estero Padre Ramos during 2012–2013. The deployment of data loggers was spread across the nesting season to represent the temporal distribution of nests. Data loggers recorded the temperature at 2 min 30 sec or at 5 min intervals, depending on the logger model, and remained in the nest during the whole incubation period until they were removed at post-hatching nest excavation. We calculated the daily mean temperature for each logger, which was then used to calculate the mean nest temperature during the whole incubation period and the mean temperature nest temperature for the middle third of incubation (i.e., thermosensitive period; Rimblot et al., 1985).

Offspring Sex Ratios and Physical Condition

Direct methods for estimating hatchling sex ratios, such as the histological evaluation of gonads, are highly accurate for sexing individual hatchlings and indirect methods—including nest temperature and incubation duration—are reliable proxies when direct methods are infeasible (Wibbels 2003). Because financial and logistical constraints prohibited us from examining the histology of dead hatchlings at Estero

Padre Ramos and from recording nest temperatures at Estero Padre Ramos in 2010–2011, we used incubation duration values obtained for offspring-producing nests to estimate primary sex ratios at both sites.

Pivotal temperature (i.e., the temperature that produces 50% of each sex; Yntema and Mrosovsky 1980) is relatively conserved among sea turtle species (Wibbels 2003) and is approximately 29.5^{o}C in hawksbills with a variation of $\pm$0.2^{o}C among studied populations (Mrosovsky et al., 2009). Incubation duration is inversely related to the temperature of the nest during the incubation period and is also inversely related to the proportion of female offspring produced in the nest (Godfrey et al., 1999). Therefore, we used published data for hawksbills that related incubation duration to sex ratio based on constant temperature incubator experiments to convert the incubation duration of each clutch into hatchling sex ratio (Godfrey et al., 1999) using the TSD program (Girondot 1999; Godfrey et al., 2003). For incubation duration calculations, the incubation period was calculated as the number of days between the date and hour of clutch deposition and the date and hour of first hatchling emergence, and included a three-day correction factor to account for the hatching-to-emergence interval (Godfrey and Mrosovsky 1997), which we estimated from nests that showed a marked temperature signal at hatching (mean = 2.9 $\pm$ 0.2 days, n = 3) (King et al., 2013). We calculated the overall sex ratio for each protection strategy between sites and among years, and used clutches deposited at half-month periods during the nesting season (Godfrey et al., 1999; Patino-Martinez et al., 2012b; Marcovaldi et al., 2014).

For all protected clutches, we recorded the following metrics for reproductive

output and hatchling physical condition: clutch size (total number of eggs), hatching success (proportion of eggs that produced live hatchlings), and straight carapace length of hatchlings measured with calipers (Bahía de Jiquilisco: Digital caliper 01407A, Neiko Tools, Taiwan; Estero Padre Ramos: Dial caliper 31-415-3, Swiss Precision Instruments, Garden Grove, CA, USA) and hatchling mass using a digital scale (Bahía de Jiquilisco: American Weigh Scales, Norcross, GA, USA) and a spring scale (Estero Padre Ramos: Micro-Line 20100, Pesola, Baar, Switzerland).

Shade Cover in Hatcheries

In Bahía de Jiquilisco and Estero Padre Ramos (2010–2013), we shaded nests in hatcheries using a variety of methods that included palm leaves, shade cloth (Bahía de Jiquilisco: Saran Verde, Freund, San Salvador, El Salvador, 75% radiation block; Estero Padre Ramos: Undetermined model, 70% radiation block), and natural forest canopy (Table 4). Shade cover from palm leaves and forest canopy over hatcheries was measured using a convex spherical densitometer (Ben Meadows, Janesville, WI, USA), except at Estero Padre Ramos in 2010–2011, where complete forest cover over the hatchery effectively represented 100% shading.

Statistical Analyses

We used a two-tailed unpaired t-test to test for differences in clutch size, hatching success, and female hatchling production between Bahía de Jiquilisco and Estero Padre Ramos. Two-way analysis of variance (ANOVA) was used to test for

differences in sand temperature within and among the beach zones, deforested area, and hatcheries between logger depths and years at Bahía de Jiquilisco. We also used a two-way ANOVA to test for differences among the three nest protection strategies in each of 10 parameters of incubation regime (i.e., nest temperature—minimum, maximum, mean of whole period, mean of thermosensitive period—during incubation, incubation duration, and nest depth) and hatchling condition (i.e., offspring sex ratios, hatching success, hatchling mass, and hatchling length) at Bahía de Jiquilisco and Estero Padre Ramos, and among years. For summary statistics, values are expressed as means $\pm$ SD. We computed all analyses using JMP Pro 11.0.0 (SAS Institute, Cary, NC, USA), with an alpha level of 0.05 where relevant.

RESULTS

Nesting Frequency and Distribution

We recorded data from 1,336 hawksbill nests during the study—466 (34.9%) located in Bahía de Jiquilisco (2011–2013) and 870 (65.1%) in Estero Padre Ramos (2010–2013). Most hawksbills nested between May and August at Bahía de Jiquilisco (n = 428, 98.4%) and Estero Padre Ramos (n = 793, 98.1%), with a peak in nesting occurring in June (n = 175, 40.2%) and July (n = 333, 41.2%), respectively (Fig. 7). Following up on anecdotal reports from local egg collectors in 2012, we verified six hawksbill nests outside of the typical nesting season during December 2013–February 2014 at Bahía de Jiquilisco. However, these nests were not included in analysis due to paucity of data.

Sand Temperature in Beach, Deforested, and Hatchery Environments

Sand temperatures at all data logger locations exhibited temporal and spatial patterns at Bahía de Jiquilisco. Temperatures generally decreased by 1–2^{o}C over the nesting season at both logger depths from April through October in the beach and deforested areas, and from May through October in hatcheries at Bahía de Jiquilisco (Fig. 8). For beach zones, temperatures generally decreased from ocean-to-forest, with the open sand >3^{o}C warmer than the woody vegetation during 2012–2013 (Fig. 9). The deforested areas and the woody vegetation beach zone logged the highest (31.66 $\pm$ 1.36^{o}C) and lowest mean seasonal temperatures (28.11 $\pm$ 0.61^{o}C), respectively, with intermediate hatchery temperatures (29.64 $\pm$ 0.86^{o}C) (Table 5). There were significant differences in temperatures between depths in all zones except open sand and non-woody vegetation, but absolute differences in temperature between 30-cm and 60-cm depths were minimal (<0.2^{o}C in all zones). Significant differences between years were detected in woody vegetation border, deforested, and hatchery zones and a marginally significant depth X year interaction in the open sand, non-woody vegetation, and woody vegetation border (Table 6). Highly significant differences in mean daily temperatures existed among the six zones and between years, with a significant zone by year interaction, at both logger depths (Table 7). In all zones, fluctuations in daily temperature were greater at the 30-cm than at the 60-cm depth, regardless of mean daily temperature (Table 5, Fig. 9).

Nest Protection Strategies

Of the 1,336 hawksbill clutches deposited at Bahía de Jiquilisco (2011–2013) and Estero Padre Ramos (2010–2013), we protected 93.0% (n = 1243) at both sites—95 (7.6%) were protected in situ, 123 (9.9%) translocated on the beach, and 1025 (82.5%) relocated to hatcheries (Fig. 10). Significantly larger clutches (t = 7.2918, df = 1238, P < 0.0001) were deposited in Bahía de Jiquilisco (170.2 eggs, SD = 35.0, n = 435) than in Estero Padre Ramos (154.4 eggs, SD = 37.3, n = 805), but hatching success was significantly lower (t = 4.0971, df = 1238, P < 0.0001) at Bahía de Jiquilisco (53.9%, SD = 33.3, n = 435; Estero Padre Ramos, 61.3%, SD = 27.6, n = 805). Of the hatchlings produced at both sites, there was a significantly higher percentage of females (t = 10.1082, df = 1135, P < 0.0001) at Bahía de Jiquilisco (84.6%, SD = 23.3, n = 373 nests) than Estero Padre Ramos (61.6%, SD = 37.2, n = 764 nests) (Fig. 7).

The thermal conditions of the nest environment, offspring sex ratios, and hatchling condition varied among protection strategies at both sites (Table 8). At Bahía de Jiquilisco, translocated and in situ nests generally had higher temperatures, lower hatching success, and a higher proportion of female offspring than nests in hatcheries. This same pattern applied to in situ and hatchery nests at Estero Padre Ramos, but translocated clutches produced a lower proportion of female hatchlings, likely because translocation occurred only in 2010–2011 when nest incubation durations were longer across all protection strategies than in 2012–2013 (Fig. 11). Differences in incubation regime parameters among strategies and between or among years were mostly insignificant—with the exception of incubation duration and nest depth at Estero Padre

Ramos—at both sites (Table 9), whereas differences in hatchling condition parameters were significant in most cases (Table 10).

DISCUSSION

Our data on sand temperatures over the nesting season in beach zones, deforested areas, and hatcheries help delineate the temporal and spatial differences in hawksbill nesting environments at Bahía de Jiquilisco. Our results indicated that sand temperatures steadily decreased over the nesting season in all sampled sites at both logger depths, with the deforested areas exhibiting a ~3^{o}C reduction in temperature between April and October (Fig. 8). This marked difference between the beginning and end of the nesting season suggests that turtles could respond to climate change through a shift in nesting phenology to exploit cooler temperatures later in the season. Additionally, turtles that currently nest in September–October at both sites and December–February at Bahía de Jiquilisco may have an adaptive advantage (Valladares et al., 2014) This highlights the importance of protecting the clutches of these individuals that utilize the margins of the season.

Similar to Kamel and Mrosovsky (2006a), we found that deforested areas were significantly warmer than forested areas and only negligible differences between sand depths in most zones. This contrasts with the results of Mrosovsky et al. (1992) for hawksbill nesting beaches in Antigua, where no differences were detected between unshaded and shaded areas, with higher reported temperatures in shaded areas toward the end of the nesting season. These marked differences in intra- and interbeach

temperatures within and among geographic regions underscore the need for site-specific data on thermal profiles to accurately assess how changes in climate and may affect nest environments of thermally sensitive species, such as hawksbills, that prefer vegetated nest-sites (Horrocks and Scott 1991; Liles et al., 2015) and utilize vegetation cover to regulate nest temperatures (Kamel 2013).

Because >80% of hawksbill clutches are relocated to hatcheries for protection at Bahía de Jiquilisco and Estero Padre Ramos, an accurate assessment of the thermal profiles in hatchery enclosures is essential for informed management. Sand temperatures in hatcheries were significantly lower at the 30-cm than the 60-cm depth and were much more pronounced than differences between sand depths in the beach zones and deforested areas (Table 5, Fig. 9). The reasons for this are unclear, but the hatchery preparation process—where sand in the hatchery enclosure is removed to a depth of 1 m, filtered through wire mesh to remove non-organic and organic material, and then replaced at the beginning of the season—may alter the composition or moisture content of the sand. However, this phenomenon has not been reported in other studies that analyzed temperature at multiple sand depths (e.g., Naro-Maciel et al., 1999). Sand temperatures in hatcheries at Bahía de Jiquilisco also differed significantly between years, which were likely influenced by the inclusion of data from an additional hatchery at Las Isletas in 2013, and by differences in ambient temperature between 2012 and 2013. Although we were unable to generate thermal profiles for the hatchery in Estero Padre Ramos, the longer overall incubation durations for nests suggest that sand temperatures were cooler than nests incubated in hatcheries at Bahía de Jiquilisco (Table

8).

Egg relocation often is used as a means to increase hatchling production around the globe (Formia et al., 2003; Garcia et al., 2003; Patino-Martinez et al., 2012a) and increasingly may be employed as a strategy to mitigate climate change (van de Merwe et al., 2006; Patino-Martinez et al., 2012b). Some studies report decreased hatching success (Garrett et al., 2010), decreased hatchling fitness (Maulany et al. 2012), and skewed primary sex ratios (Chan and Liew 1995) for manipulated clutches. Other studies, however, find that relocated clutches have higher hatching success and lower proportion of female offspring than natural nests (Garcia et al., 2003; Kornaraki et al., 2006; Wood et al., 2014). At Bahía de Jiquilisco and Estero Padre Ramos, we found minimal differences among the three nest protection strategies and among years in thermal conditions of the nest environment, but many significant differences in offspring sex ratios, hatchling condition, and nest depth (Table 10). It is important to note that nest temperatures were not recorded at Estero Padre Ramos in 2010–2011, wherein nest incubation durations were considerably longer (Fig. 11), suggesting that nest temperatures were substantially lower for all nest protection strategies during this period. This difference between the period of 2010–2011 and 2012–2013 may be partly accounted for by the change in hatchery location from a site with 100% overstory vegetation cover to an area with slightly less cover (~98%) (Table 4), but the fact that longer incubation durations were recorded across protection strategies at Estero Padre Ramos suggests that climatic factors—such as cooler ambient temperature and decreased precipitation—may have contributed.

One of our most striking findings is the relatively low hatching success (58.5 ± 30.1%, n = 1240 nests) across all protection strategies at Bahía de Jiquilisco and Estero Padre Ramos compared to hawksbills in the Caribbean (e.g., 91.6%, Bjorndal et al., 1985; 84.5%, Horrocks and Scott 1991; 78.6%, Ditmer and Stapleton 2012) and Indo-Pacific (90.1% [emergence success], Limpus 1980; 79.9% [emergence success], Loop et al., 1995; 82.4%, Dobbs et al., 1999). Further, we found significantly lower hatching success for in situ clutches (46.9 ± 30.0%, n = 93) than for clutches relocated to hatcheries (60.9 ± 29.2%, n = 1025) at both sites (Table 8). This difference between in situ and hatchery clutches could arise from the amount of organic content in the sand, which is potentially lower in hatcheries given that organic material is removed during the preparation process. This is consistent with the results of Ditmer and Stapleton (2012), who found that hatching success increased as a function of decreasing organic content in the sand for hawksbill clutches in Antigua, West Indies. We suspect the differences in overall hatching success reflect the distinct biophysical conditions of our study sites, such as presence of extremely fine-grained sand on nesting beaches. For example, nesting beaches in Bahía de Jiquilisco consist of a high proportion of sand particle sizes measuring ≤0.063 mm (Y. Flores, unpublished data), which is substantially smaller than sand grain sizes reported for hawksbill nesting beaches in other geographic regions (e.g., Dobbs et al., 1999; Ditmer and Stapleton 2012; Zare et al., 2012). Because sand grain size affects water and gas flux (Ackerman 1980), sand consisting of extremely small particle sizes could have high water content (Foley et al., 2006) and inhibit respiratory gas exchange of developing embryos (Ackerman 1997), which could

lower hatching success. The selection of nest sites on beaches in mangrove estuaries may represent a tradeoff between higher survival rates of adults in estuarine waters and lower hatchling production in sub-optimal nest environments.

We estimate that hawksbill nesting beaches produced ~70% female hatchlings at our study sites, with a higher percentage of females produced at Bahía de Jiquilisco than Estero Padre Ramos (Table 8). Our results represent lower female-biased sex ratios than reported at sea turtle nesting beaches in other ocean basins (Wibbels 2003; Hawkes et al., 2009), where sex ratios are heavily skewed toward females in many populations (Wibbels et al., 1999; Broderick et al., 2000; Marcovaldi et al., 2014). There were large differences in sex ratios among strategies and among years, particularly in Estero Padre Ramos (Table 10; Fig. 7). Because our sex ratio estimate is a function of incubation duration, it is not surprising that the percentage of female hatchlings produced were much lower in Estero Padre Ramos in 2010–2011 than in 2012–2013. Additionally, clutches were translocated in Estero Padre Ramos only in 2010 and 2011, which explains the large difference detected among nest protection strategies. We primarily attribute the higher percentage of females produced at Bahía de Jiquilisco to the degraded condition of coastal forest at many beaches relative to the higher-quality habitat that is available to nesting turtles at Estero Padre Ramos (Liles et al., 2015), particularly at areas where nests are protected in situ. Indeed, Kamel (2013) found that vegetation cover predicts nest temperatures, which highlights the importance of preserving and restoring natural vegetation cover at hawksbill nesting beaches.

Hatchling length and mass differed among nest protection strategies and among

years (Table 10), with in situ nests overall producing smaller hatchlings (Table 8). Given incongruences in measurement equipment, caution should be used when comparing values of length and mass between sites. However, values within sites represent real differences among nest protection strategies and among years, and demonstrate that hatchlings from in situ nests had smaller lengths and masses. Previous studies indicate that nest temperature is inversely correlated with hatchling length, where warmer nests produce hatchlings with smaller carapaces, but that nest temperature did not influence hatchling mass (Maulany et al., 2012; Booth et al., 2013; Wood et al., 2014). Hatchlings with larger carapaces are likely to crawl faster and employ more thrust while swimming than smaller hatchlings (Janzen et al., 2000; Ischer et al., 2009). This suggests that hatchlings from in situ nests may be at a disadvantage compared to hatchlings from translocated and hatchery clutches, whose larger size may allow them to more quickly navigate away from near-shore predators to offshore waters and thus increase their chance of survival (Wood et al., 2014).

Our findings suggest that adjustment of nest depth by hawksbills is unlikely to compensate for climate change in mangrove estuaries. First, minimal differences in sand temperature (<0.2^{o}C) exist between 30-cm and 60-cm depths in all beach zones. Second, groundwater is present at a depth of 50–85 cm during the nesting season at many beaches, which can be expected to become shallower as sea levels rise and further constrict suitable nest environments. This likely explains—at least in part—why hawksbills construct shallower nest cavities in Bahía de Jiquilisco (38.7 cm) and Estero Padre Ramos (40.9 cm) than at open-coast nesting locations (e.g., 45.3 cm, Loop et al.,

1995; 47.0 cm, Kamel and Mrosovsky 2006a). Finally, hatching success and male hatchling production decrease as a function of increasing nest depth. Therefore, shifts in nesting phenology or in the selection of overstory vegetation cover may be more likely to align thermal conditions of the nest environment with a changing climate. However, mangrove ecosystems are among the most threatened tropical environments in the world, with deforestation rates as high as 3.6% per year in the Americas (Valiela et al., 2001), suggesting that future degradation of forest habitat may impair its ability to buffer against increasing temperatures. Coastal forests at our study sites are confronted with the persistent threat of conversion by competing land-uses, and forests along nesting beaches at Bahía de Jiquilisco have already experienced substantial alteration, which can be expected to increase as human populations rise. Based on our findings, in situ clutches at both sites currently incubate at higher temperatures, obtain a lower hatching success, produce a higher percentage of female hatchlings, and produce smaller hatchlings than clutches relocated to hatcheries. We are not suggesting egg relocation as a panacea that should be employed without careful consideration of local conditions, species biology, and conservation objectives. However, we contend that egg relocation can contribute significantly to recovery efforts under appropriate circumstances. Our results underscore the importance of empirical assessments to evaluate potential mitigation strategies for severely depleted populations of highly endangered species that may be unable to sufficiently respond to climate change.

CHAPTER V

CONCLUSION

Hawksbill turtles and coastal residents co-exist at nesting beaches in El Salvador and Nicaragua. Despite their critically endangered status, impoverished local residents often view hawksbill eggs as an economic resource, but speak of deeper cultural connects to the turtles. There is a general disconnect between the priorities of the international conservation community, which focuses on the biological aspects of hawksbills, and local residents, who tend to prioritize the socio-economic development and needs of human communities. The purchase of hawksbill eggs collected by local community members for protection in hatcheries offers an avenue for increasing local participation in conservation while simultaneously improving human wellbeing in areas where employment opportunities are scarce. Enhancing opportunities and fueling interest for local participation in conservation is particularly important in El Salvador and Nicaragua, where the majority of eastern Pacific hawksbill nesting occurs. Additionally, community-supported hatcheries may provide a thermal refuge for the incubation of hawksbill eggs if behavioral plasticity in nesting is unable to compensate for forecasted climate change. Harmonizing international conservation priorities with local community development realities is one path towards simultaneously contributing to long-term hawksbill turtle recovery and human wellbeing in low-income regions.

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APPENDIX A

FIGURES

Figure 1. Hawksbill Nesting Sites (Circles) along the Coast of El Salvador (Liles et al., 2014).

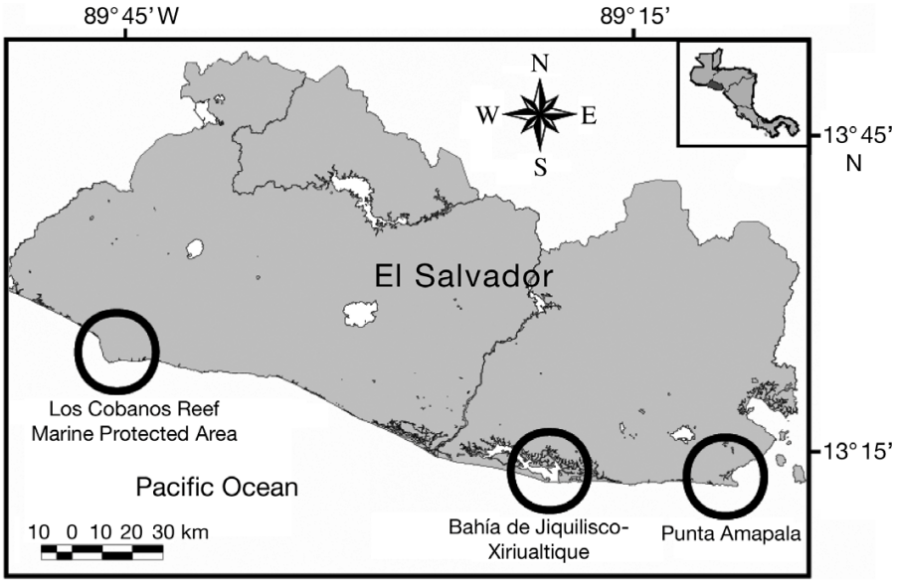


Figure 2. Locations of Hawksbill Nesting Beaches (Dots and Lines), Hatcheries (Circles), and in situ Nest Protection Areas (Diamonds) in (a) Bahía de Jiquilisco, El Salvador and (b) Estero Padre Ramos, Nicaragua (Liles et al., 2015).

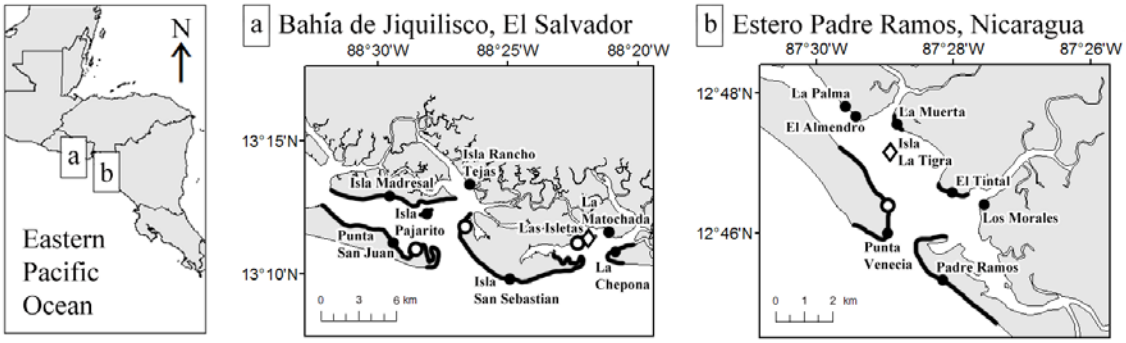


Figure 3. Distribution (±95% CI) of Hawksbill Nests among Four Beach Zones in Bahía de Jiquilisco, El Salvador (*n* = 405), and Estero Padre Ramos, Nicaragua (n = 289), 2011–2013. OS, Open Sand; NWV, Non-woody Vegetation; WVB, Woody Vegetation Border; WV, Woody Vegetation. Values above Error Bars Represent Number of Nests (Liles et al., 2015).

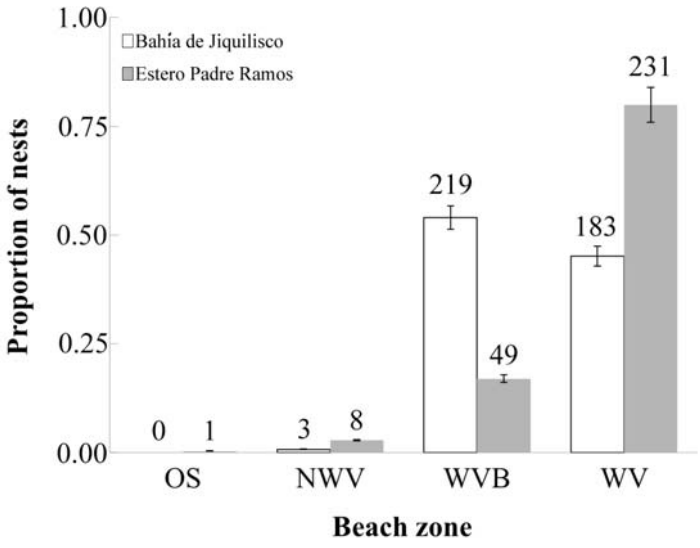
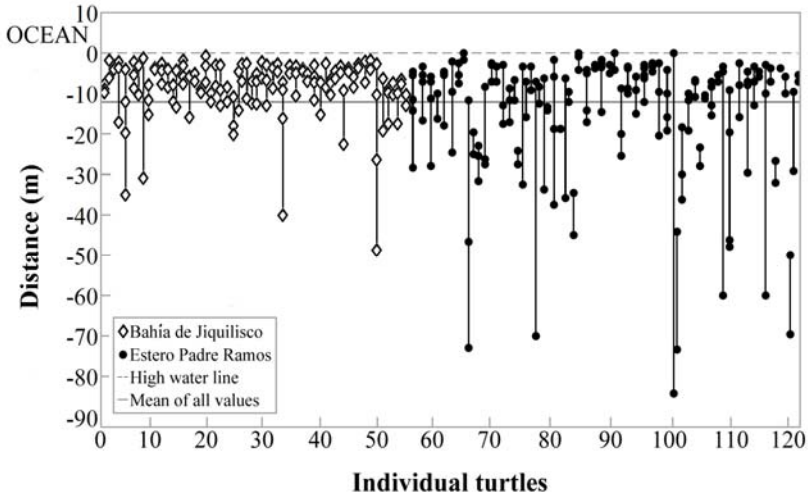


Figure 4. Repeatability of Nest Sites Selected by Hawksbills with ≥2 Nests per Year Relative to the (a) Distance from the Current High Water Line (r = 0.07, P = 0.2250, Bahía de Jiquilisco; r = 0.34, P < 0.0001, Estero Padre Ramos), (b) Distance from the Woody Vegetation Border (r = –0.10, P = 0.8483, Bahía de Jiquilisco; r = 0.11, P = 0.0796, Estero Padre Ramos) and (c) Overstory Vegetation Cover above Nests (r = 0.62, P < 0.0001, Bahía de Jiquilisco; r = 0.68, P < 0.0001, Estero Padre Ramos) in Bahía de Jiquilisco, El Salvador (n = 57 Turtles and 145 Nests) and Estero Padre Ramos, Nicaragua (n = 66 Turtles and 185 Nests), 2011–2013. Solid Horizontal Lines Represent the Mean of All Values and Negative Numbers Indicate the Landward Distance from Current High Water Line in (a) and from Woody Vegetation Border in (b). Nests below the Dashed Line in (c) Were in Woody Vegetation and Nests above Were Not (Liles et al., 2015).

(a) Nest to Current High Water Line



(b) Nest to Woody Vegetation Border

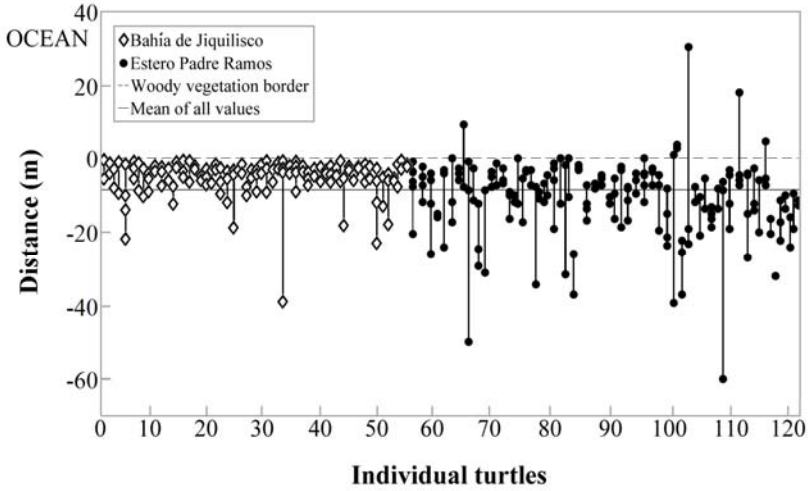


Figure 4. Continued.

(c) Overstory Vegetation Cover

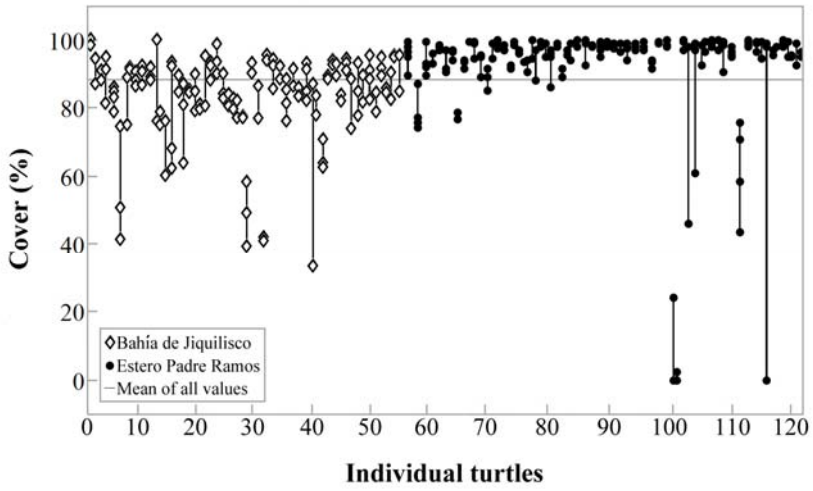


Figure 5. Aerial and Ground Level Images of the Primary Inshore Beaches Used by Nesting Hawksbills in (a) Bahía de Jiquilisco, El Salvador, and (b) Estero Padre Ramos, Nicaragua, 2013 (Liles et al., 2015).

(a) Bahía de Jiquilisco

(b) Estero Padre Ramos

Figure 6. Locations of Hawksbill Nesting Beaches, Hatcheries, and in situ Nest Protection Areas in (a) Bahía de Jiquilisco, El Salvador and (b) Estero Padre Ramos, Nicaragua.

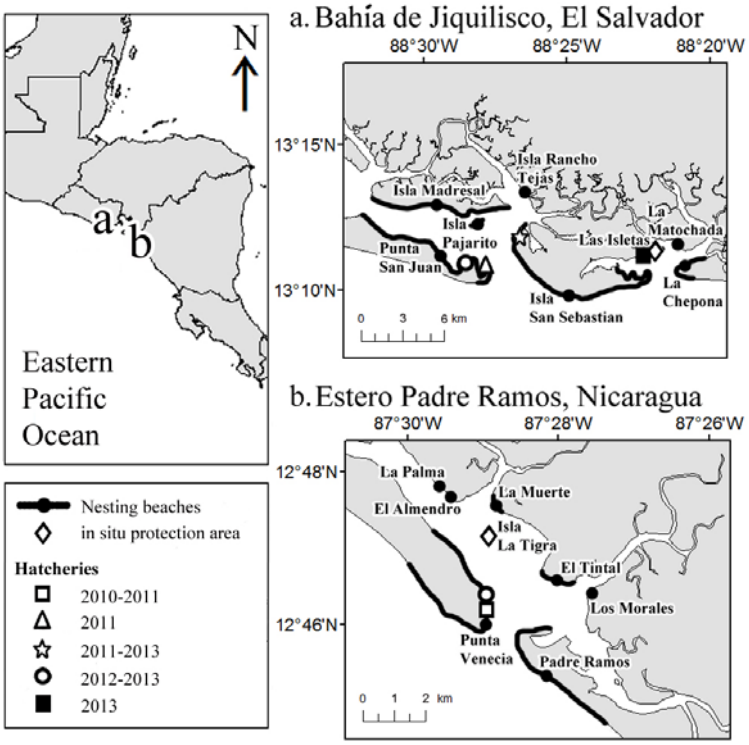
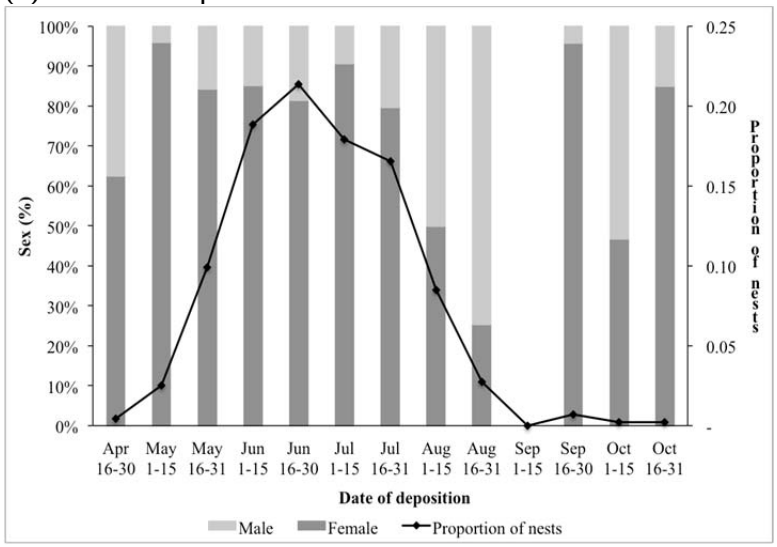


Figure 7. Frequency Distribution of Hawksbill Nesting and Estimated Offspring Sex Ratios from Three Nest Protection Strategies at (a) Bahía de Jiquilisco, El Salvador (*n* = 435 Nests), 2011–2013 and (b) Estero Padre Ramos, Nicaragua (*n* = 808 Nests), 2010–2013.

(a) Bahía de Jiquilisco



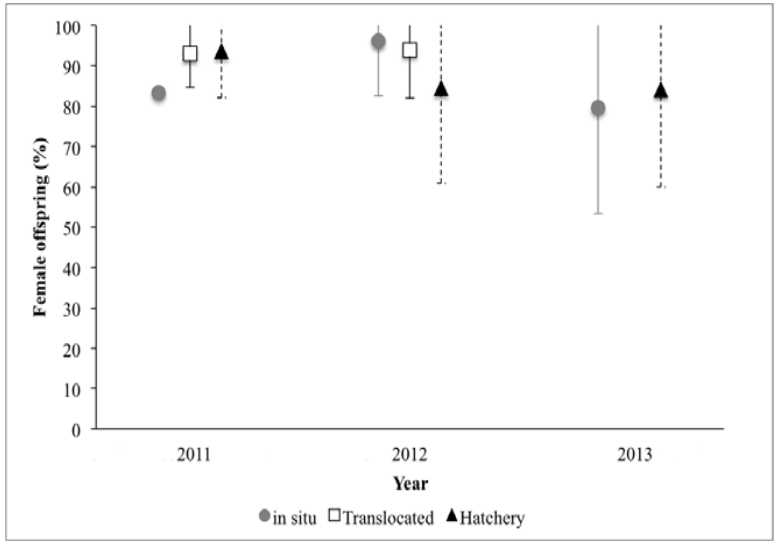
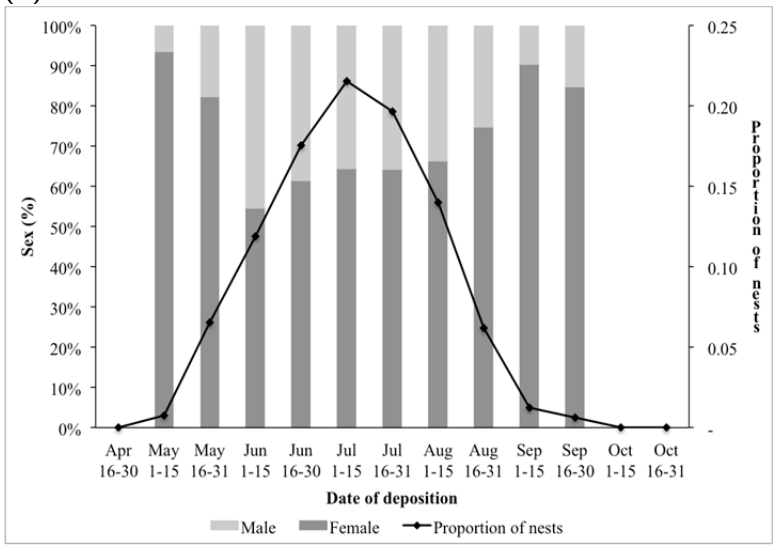


Figure 7. Continued.

(b) Estero Padre Ramos



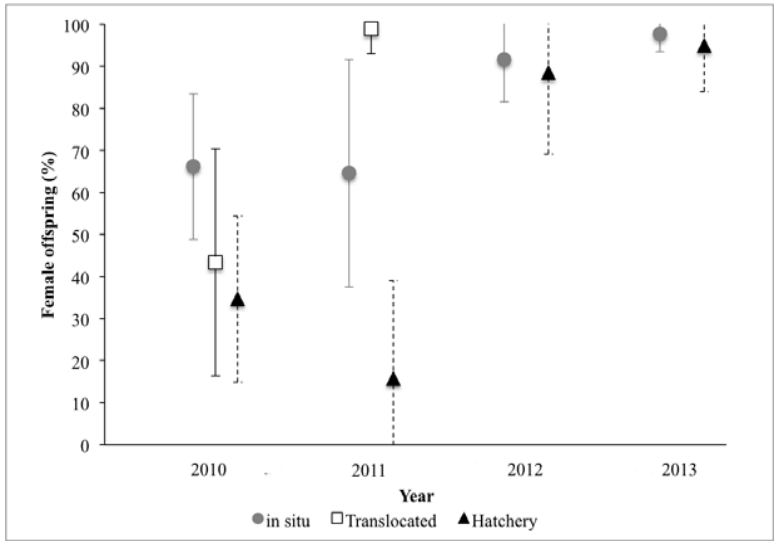


Figure 8. Daily Sand Temperatures (± SD) at Two Depths over the Hawksbill Nesting Season at (a) Las Isletas Beach (*n* = 24 Loggers), (b) Deforested Areas at Las Isletas Beach (*n* = 12 Loggers), and (c) in Hatcheries (*n* = 7 Loggers) at Bahía de Jiquilisco, El Salvador, 2012–2013. Data Collection Occurred from 1 April through 31 October for (a) and (b), and from 1 May through 31 October for (c).

(a) Beach

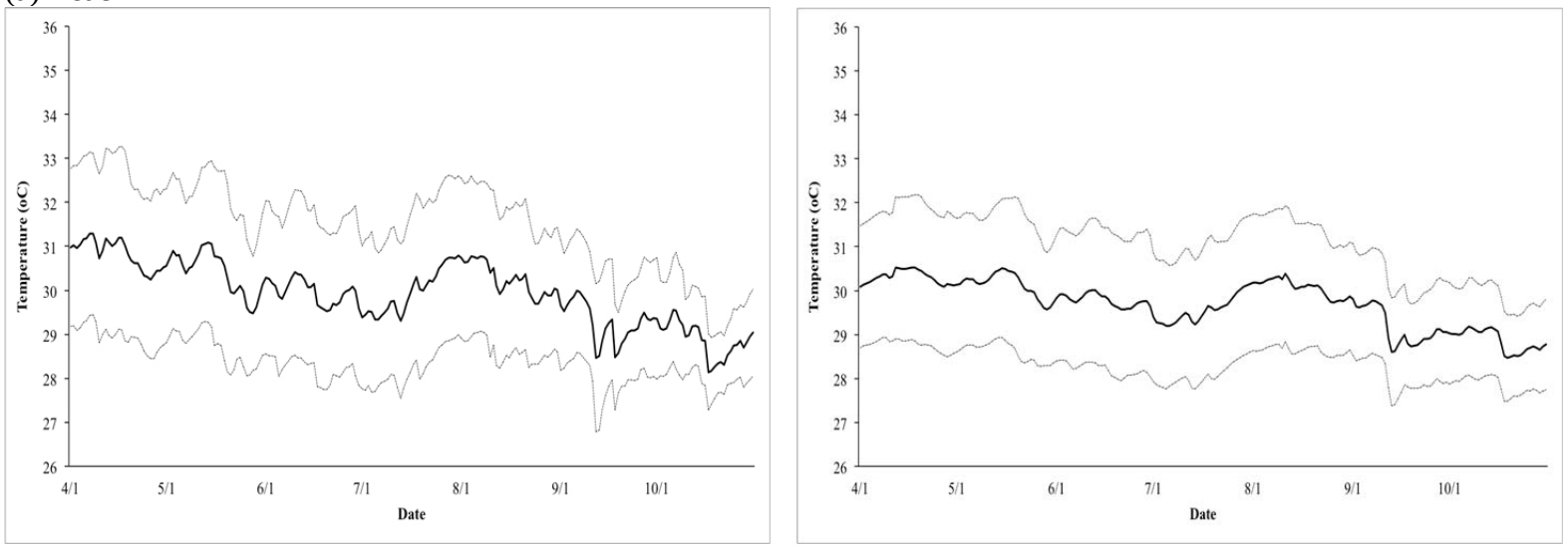


Figure 8. Continued.

(b) Deforested

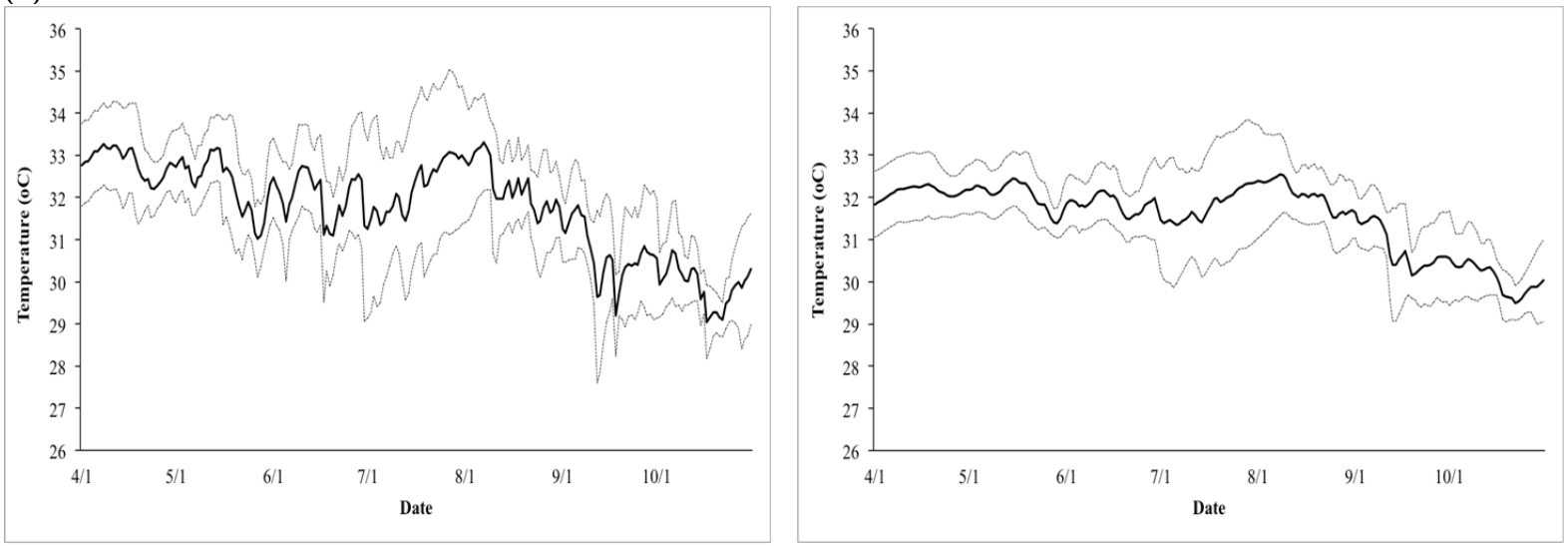
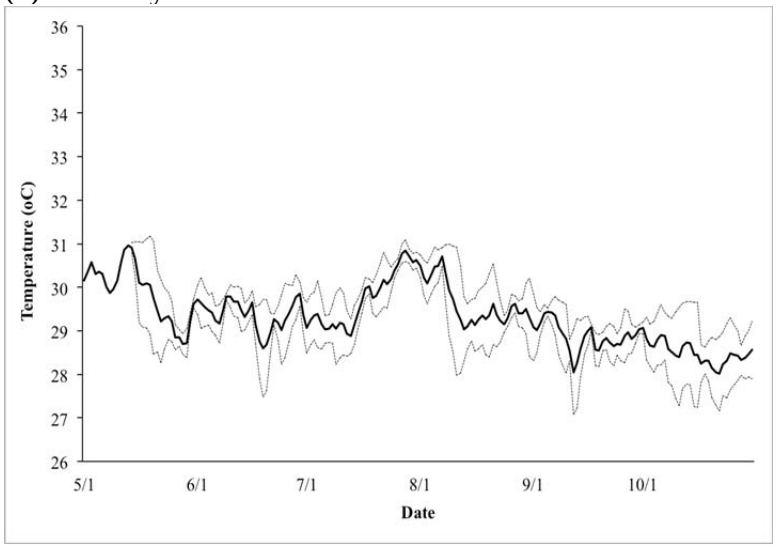


Figure 8. Continued.

(c) Hatchery



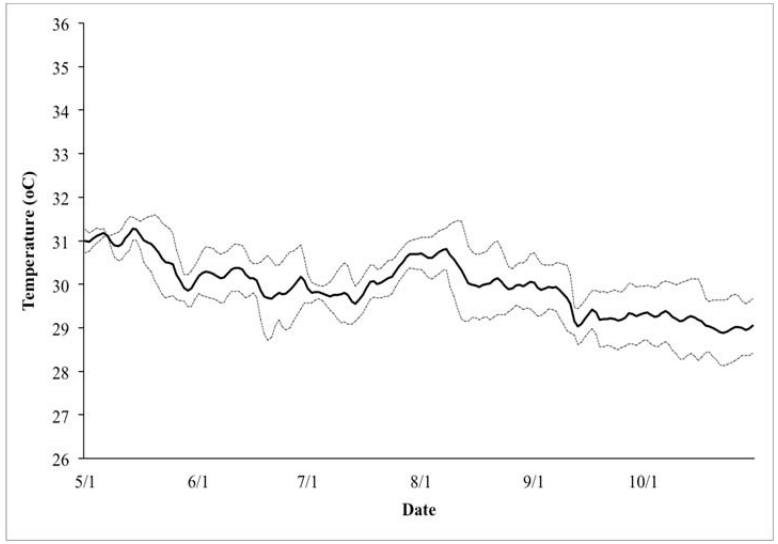


Figure 9. Sand Temperature (Mean ± SD) at Two Depths over the Hawksbill Nesting Season in Four Vegetative Zones and Deforested Areas of Las Isletas Beach, and in Hatcheries at Bahía de Jiquilisco, El Salvador, 2012–2013. Data Collection Occurred from 1 April through 31 October in the Four Vegetative Zones (Open Sand, n = 8 Loggers; Non-woody Vegetation, n = 4) and Deforested Areas (n = 12), and from 1 May through 31 October in Hatcheries (n = 7).

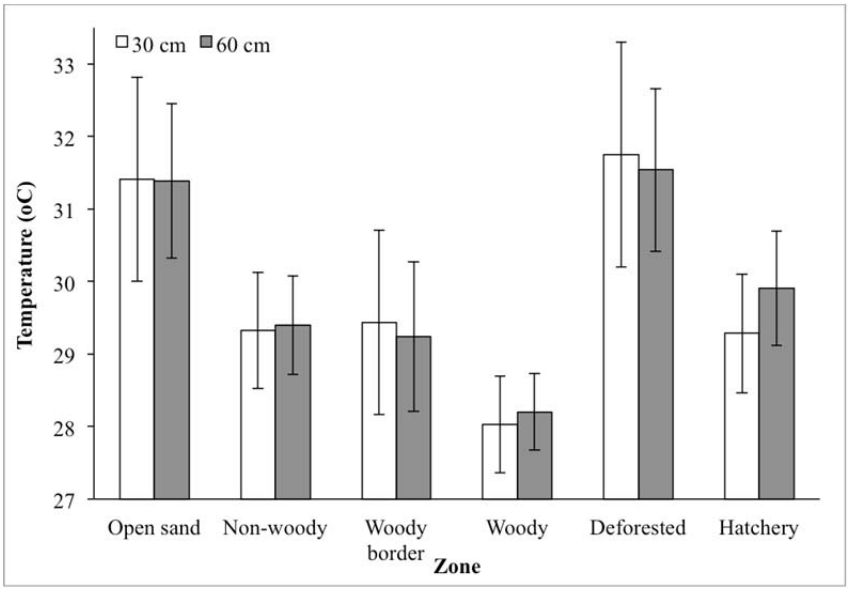
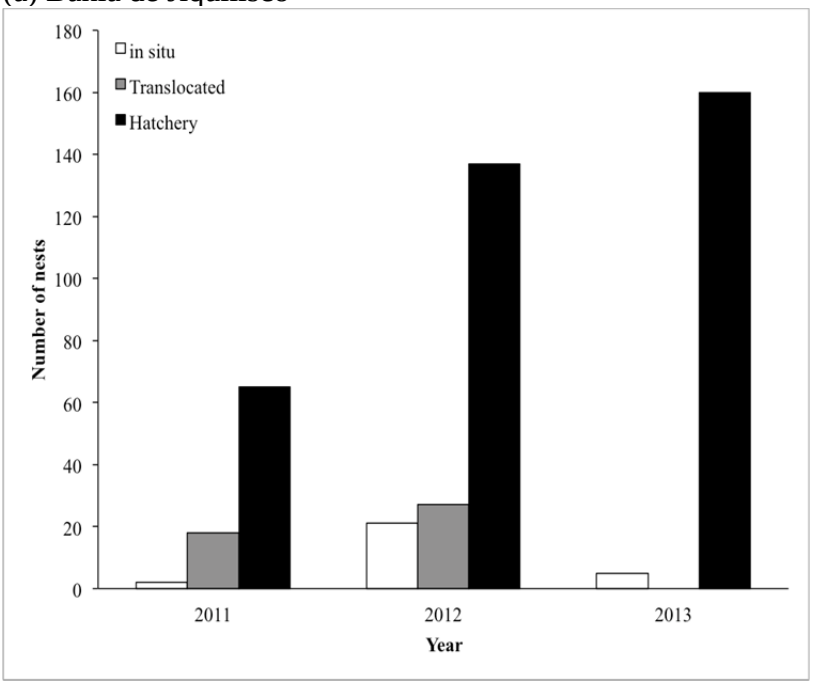


Figure 10. Number of Hawksbill Nests Protected Using the Three Protection Strategies in (a) Bahía de Jiquilisco, El Salvador (*n* = 435), 2011–2013 and (b) Estero Padre Ramos, Nicaragua (*n* = 808), 2010–2013.

(a) Bahía de Jiquilisco



(b) Estero Padre Ramos

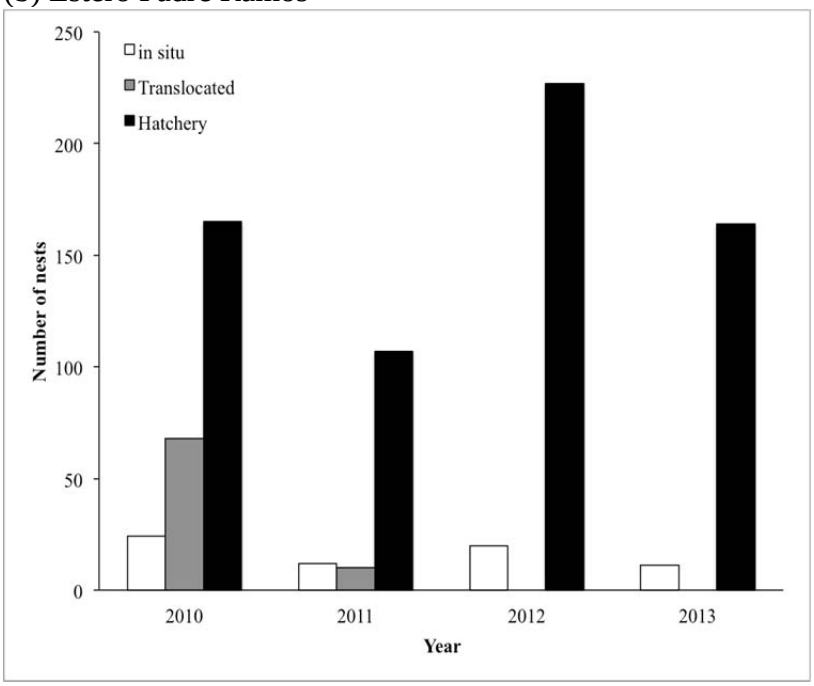
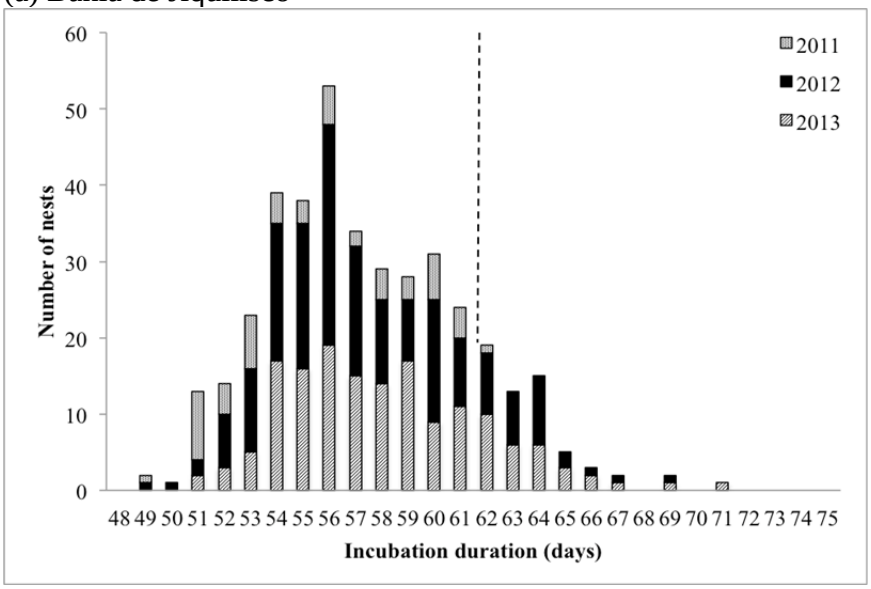
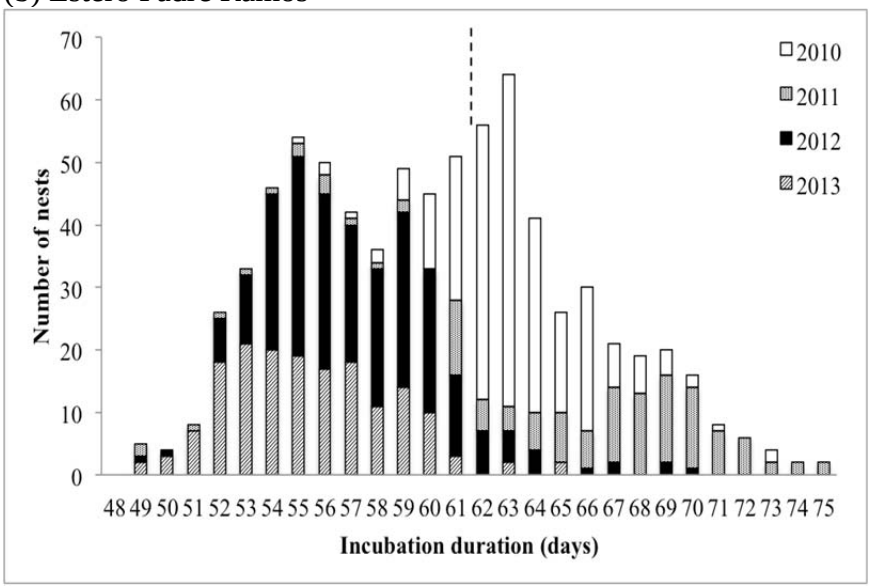


Figure 11. Incubation Durations of Hawksbills at (a) Bahía de Jiquilisco, El Salvador (*n* = 373), 2011–2013 and (b) Estero Padre Ramos, Nicaragua (*n* = 764), 2010–2013. Dashed Vertical Line Represents the Mean Pivotal Incubation Duration for Hawksbills (Godfrey et al., 1999).

(a) Bahía de Jiquilisco



(b) Estero Padre Ramos



APPENDIX B

TABLES

Table 1. Chronology of Sea Turtle Egg Protection and Hatchery Management in El Salvador (Liles et al., 2014).

Year	Description	Legal Framework
1975	First use of hatcheries for sea turtle nest protection	None
1994	Wildlife Conservation Law regulates the sustainable use of wildlife	República de El Salvador 1994b
1997	Penal Code sanctions 3–5 years in prison for predation of protected species	República de El Salvador 1997
1997	Ban on consumption of leatherback eggs; mandatory donation of up to 24 eggs per nest of all species to hatcheries; remaining eggs can be legally sold for consumption	Ministry of Agriculture and Livestock (MAG) 1997
2009	Ban on consumption of eggs of all sea turtle species; eggs can be legally collected and sold to hatcheries	República of El Salvador 2009
2010	Guidelines for the management of sea turtle hatcheries	Ministry of the Environment and Natural Resources (MARN) 2010

Table 2. Comparison of the Five Best-supported Predictive Models for Beach Zone Selection by Nesting Female Hawksbills in Bahía de Jiquilisco, El Salvador and Estero Padre Ramos, Nicaragua in 2011–2013 (n = 694 Nests) (Liles et al., 2015).

Rank[a]	Predictor variables[b]	K[c]	AIC_c[d]	Δ_i[e]	w_i[f]	w_1/w_i[g]	AUC[h]			
							OS	NWV	WVB	WV
1	WVB + OVC + HWL + Site + Year	7	749.4	0.0	0.793	1.00	1.00	1.00	0.81	0.82
2	WVB + OVC + Site + Year	6	753.0	3.6	0.133	5.95	1.00	1.00	0.81	0.81
3	WVB + HWL + Site + Year	6	754.7	5.3	0.057	13.82	1.00	1.00	0.81	0.81
4	WVB + Site + Year	5	757.4	8.0	0.015	53.87	1.00	1.00	0.80	0.81
5	WVB + OVC + HWL + Year	6	763.2	13.7	0.001	946.24	1.00	1.00	0.80	0.81

[a]Model ranked 1 is the best-approximating model according to AIC_c among those considered. Models ranked 1–3 constitute the 95% confidence set based on summed w_i (Burnham et al., 2011).
[b]Intercept is included in all models. Predictor variable definitions: WVB, distance from nest to woody vegetation border; OVC, percentage of overstory vegetation cover above nest; HWL, distance from nest to current high water line; site, geographic area where nest was laid, Bahía de Jiquilisco in El Salvador or Estero Padre Ramos in Nicaragua; year, year in which nest was laid (2011–2013). Curved carapace length of female turtle was not included in models.
[c]Number of parameters in model.
[d]Akaike's information criterion corrected for small sample size.
[e]Delta AIC_c, difference in AIC_c value from best-approximating model.
[f]Akaike weight, probability that current model is best-approximating model among those considered.
[g]Evidence ratio, relative likelihood of each model in relation to best-approximating model.
[h]AUC is the area under the receiver operating characteristic curve for four response variable categories: OS, nest placed in open sand; NWV, nest placed in non-woody vegetation; WVB, nest placed in woody vegetation border; WV, nest placed in woody vegetation.

Table 3. Comparison of the Six Best-supported Predictive Models for Beach Zone Selection by Nesting Female Hawksbills Where the Curved Carapace Length Was Measured in Bahía de Jiquilisco, El Salvador and Estero Padre Ramos, Nicaragua in 2011–2013 (n = 387 Nests) (Liles et al., 2015).

Rank[a]	Predictor variables[b]	K[c]	AIC_c[d]	Δ_i[e]	w_i[f]	w_1/w_i[g]	AUC[h]			
							OS	NWV	WVB	WV
1	WVB + OVC + Year	5	415.4	0.0	0.375	1.00	1.00	1.00	0.79	0.80
2	WVB + OVC + HWL+ Year	6	415.8	0.4	0.305	1.23	1.00	1.00	0.80	0.81
3	WVB + HWL + Site + Year	6	416.7	1.3	0.199	1.88	1.00	1.00	0.80	0.81
4	WVB + OVC + HWL + Site + Year	7	420.5	5.1	0.029	13.12	1.00	1.00	0.80	0.81
5	WVB + OVC + Site + Year	6	420.7	5.3	0.026	14.47	1.00	1.00	0.79	0.80
6	WVB + OVC + CCL + Year	6	421.9	6.5	0.014	26.06	1.00	1.00	0.79	0.80

[a]Model ranked 1 is the best-approximating model according to AIC_c among those considered. Models ranked 1–6 constitute the 95% confidence set based on summed w_i (Burnham et al., 2011).
[b]Intercept is included in all models. Predictor variable definitions: WVB, distance from nest to woody vegetation border; OVC, percentage of overstory vegetation cover above nest; HWL, distance from nest to current high water line; CCL, curved carapace length of female turtle; site, geographic area where nest was laid, Bahía de Jiquilisco in El Salvador or Estero Padre Ramos in Nicaragua; year, year in which nest was laid (2011–2013).
[c]Number of parameters in model.
[d]Akaike's information criterion corrected for small sample size.
[e]Delta AIC_c, difference in AIC_c value from best-approximating model.
[f]Akaike weight, probability that current model is best-approximating model among those considered.
[g]Evidence ratio, relative likelihood of each model in relation to best-approximating model.
[h]AUC is the area under the receiver operating characteristic curve for four response variable categories: OS, nest placed in open sand; NWV, nest placed in non-woody vegetation; WVB, nest placed in woody vegetation border; WV, nest placed in woody vegetation.

Table 4. Information on Nest Protection Strategies for Hawksbill Turtles in Bahía de Jiquilisco, El Salvador, 2011–2013 and Estero Padre Ramos, Nicaragua, 2010–2013.

Site Location	Year	Size (m^2)	Shade (%)	Shading materials
Bahía de Jiquilisco				
PSJ	2011	100	52.4 ± 2.2	Palm leaves
	2012–2013	100	96.3 ± 4.5	Shade cloth; forest canopy
LP	2011–2013	50	84.5 ± 7.2	Shade cloth; forest canopy
LI	2013	50	90.1 ± 3.8	Shade cloth; forest canopy
Estero Padre Ramos				
PV	2010–2011	125	100.0	Shade cloth; forest canopy
	2012–2013	125	77.7 ± 16.4	Shade cloth; forest canopy

Table 5. Mean (± SD) Sand Temperature (°C) at Two Depths over the Hawksbill Nesting Season in Four Vegetative Zones and Deforested Areas of Las Isletas Beach, and in Hatcheries at Bahía de Jiquilisco, El Salvador, 2012–2013. Data Collection Occurred from 1 April through 31 October in the Four Vegetative Zones and Deforested Areas, and from 1 May through 31 October in Hatcheries.

	2012						2013					
	30 cm			60 cm			30 cm			60 cm		
Zone	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
Open sand	31.31	1.19	620	31.49	0.69	214	31.55	1.66	428	31.34	1.21	428
Non-woody	29.31	0.59	214	29.50	0.33	171	29.34	0.97	214	29.31	0.85	214
Woody border	28.89	0.97	428	28.80	0.72	427	29.99	1.30	428	29.70	1.10	426
Woody	27.96	0.47	214	28.22	0.33	132	28.10	0.81	214	28.19	0.62	214
Deforested	32.15	1.37	642	31.93	0.89	642	31.36	1.63	642	31.15	1.20	642
Hatchery	29.06	0.77	342	29.55	0.64	342	29.69	0.76	184	30.24	0.78	368

Table 6. Two-way ANOVA Results for Differences in Sand Temperature between Logger Depths (30 and 60 cm), between Years (2012–2013), and with Interactions between Zone and Year for Each of Four Beach Zones, Deforested Area, and Hatchery at Bahía de Jiquilisco, El Salvador.

Zone Source	df	SS	MS	F	*P*
Open sand					
Depth	1	5.2973	5.2973	3.2165	0.0731
Year	1	15.5145	15.5145	9.4202	0.0022
Depth X Year	1	14.3720	14.3720	8.7265	0.0032
Error	1686	2776.7477	1.6469		
Total	1689	2795.5750	1.6552		
Non-woody					
Depth	1	3.3329	3.3329	6.0217	0.0143
Year	1	0.0898	0.0898	0.1623	0.6872
Depth X Year	1	2.3617	2.3617	4.2669	0.0392
Error	809	447.7693	0.5535		
Total	812	452.1559	0.5568		
Woody border					
Depth	1	1.5114	1.5114	1.3876	0.2390
Year	1	258.4363	258.4363	237.2780	<0.0001
Depth X Year	1	4.5142	4.5142	4.1447	0.0419
Error	1705	1857.0368	1.0890		
Total	1708	2300.6664	1.3470		
Woody					
Depth	1	5.3039	5.3039	14.4166	0.0002
Year	1	1.9371	1.9371	5.2652	0.0220
Depth X Year	1	1.2300	1.2300	3.3433	0.0679
Error	770	283.2836	0.3680		
Total	773	290.8177	0.3762		
Deforested					
Depth	1	15.3846	15.3846	9.1326	0.0025
Year	1	199.2280	199.2280	118.2662	<0.0001
Depth X Year	1	0.0081	0.0081	0.0048	0.9446
Error	2564	4319.2443	1.685		
Total	2567	4743.8906	1.8480		
Hatchery					
Depth	1	40.9704	40.9704	75.7192	<0.0001
Year	1	46.6992	46.6992	86.3068	<0.0001
Depth X Year	1	0.2659	0.2659	0.4914	0.4835
Error	1232	666.6151	0.5411		
Total	1235	915.2311	0.7411		

Table 7. Two-way ANOVA Results for Differences in Sand Temperature among Six Zones (Open Sand, Non-woody Vegetation, Woody Vegetation Border, Woody Vegetation, Deforested Area, and Hatchery), between Years (2012–2013), and with Interactions between Zone and Year for Two Logger Depths (30 and 60 cm) at Bahía de Jiquilisco, El Salvador.

Depth Source	df	SS	MS	F	*P*
30 cm					
Zone	5	5568.7177	1113.7435	742.5468	<0.0001
Year	1	46.7742	46.7742	31.1850	<0.0001
Zone X Year	5	505.1250	101.025	67.3546	<0.0001
Error	4558	6836.529	1.500		
Total	4569	15116.978	3.3086		
60 cm					
Zone	5	3831.6754	766.3351	917.6392	<0.0001
Year	1	4.3387	4.3387	5.1953	0.0227
Zone X Year	5	455.4031	91.0801	109.0634	<0.0001
Error	4208	3514.1676	0.835		
Total	4219	9587.5438	2.2725		

Table 8. Values (± SD) for Ten Parameters of Incubation Regime and Hatchling Condition for Each of Three Hawksbill Nest Protection Strategies at Bahía de Jiquilisco, El Salvador, 2011–2013 and Estero Padre Ramos, Nicaragua, 2010–2013.

Site	Incubation regime[c]						Hatchlings			
Strategy	Min temp (°C)	Max temp (°C)	Mean temp (°C)	Mean temp, TP[d] (°C)	Duration (d)	Nest depth[c] (cm)	Hatching[e] (%)	Female[c,f] (%)	Mass[e] (g)	Length[e] (cm)
Bahía de Jiquilisco										
in situ	26.4 ± 1.4 (11)	34.8 ± 2.8 (11)	30.7 ± 1.3 (11)	30.4 ± 1.5 (11)	55.9 ± 3.9 (22)	38.7 ± 2.9 (28)	32.1 ± 27.7 (28)	91.1 ± 18.5 (22)	11.1 ± 1.3 (303)	3.7 ± 0.3 (203)
Translocated[a]	26.7 ± 0.7 (15)	35.2 ± 2.0 (15)	30.8 ± 1.0 (15)	30.5 ± 1.0 (15)	55.5 ± 3.7 (33)	36.7 ± 3.3 (45)	39.1 ± 32.8 (45)	93.6 ± 11.0 (33)	11.5 ± 1.2 (400)	3.7 ± 0.2 (466)
Hatchery	26.6 ± 1.2 (88)	33.7 ± 1.9 (88)	30.0 ± 1.2 (88)	29.7 ± 1.3 (88)	57.3 ± 3.7 (318)	38.7 ± 3.5 (362)	57.3 ± 32.6 (362)	84.9 ± 23.3 (318)	11.4 ± 1.2 (5723)	3.8 ± 0.2 (5023)
Estero Padre Ramos										
in situ	27.2 ± 1.4 (13)	33.6 ± 1.1 (13)	30.3 ± 0.7 (13)	30.1 ± 0.9 (13)	58.2 ± 3.4 (64)	40.9 ± 4.1 (35)	55.2 ± 28.0 (65)	78.6 ± 21.5 (64)	11.3 ± 1.0 (200)	3.7 ± 0.2 (141)
Translocated[b]	–	–	–	–	61.6 ± 4.3 (68)	43.8 ± 4.9 (25)	50.3 ± 30.8 (77)	49.1 ± 30.7 (68)	12.3 ± 1.5 (807)	3.7 ± 0.2 (837)
Hatchery	27.3 ± 1.2 (38)	33.3 ± 1.4 (38)	30.1 ± 0.8 (38)	29.8 ± 1.0 (38)	59.8 ± 5.5 (632)	43.3 ± 5.2 (592)	63.1 ± 26.8 (663)	65.4 ± 37.0 (632)	12.3 ± 1.5 (9426)	3.7 ± 0.2 (9554)

[a]Excludes year 2013.
[b]Excludes years 2012–2013.
[c]Values in parentheses represent the number of nests.
[d]TP, thermosensitive period.
[e]Values in parentheses represent the number of hatchlings.
[f]Includes 3 day correction factor for hatchling emergence.

Table 9. Two-way ANOVA Results for Differences in Each of Six Incubation Regime Variables among Three Nest Protection Strategies (in situ, Translocated on Beach, and Hatchery), between or among Years, and with Interactions between Strategy and Year at Bahía de Jiquilisco, El Salvador (2011–2013) and Estero Padre Ramos, Nicaragua (2010–2013).

Incubation regime	Bahía de Jiquilisco					Estero Padre Ramos				
Source	df	SS	MS	F	*P*	df	SS	MS	F	*P*
Minimum temperature										
Strategy	2	0.3603	0.1802	0.1335	0.8752	1	0.4610	0.4610	0.2744	0.6029
Year	1	0.2079	0.2079	0.1541	0.6955	1	0.3245	0.3245	0.1931	0.6623
Strategy X Year	3	5.3162	1.7720	1.3129	0.2741	1	1.4606	1.4606	0.8692	0.3559
Error	106	143.0733	1.3498			47	78.9781	1.6804		
Total	113	148.8046	1.3169			50	80.5238	1.6105		
Maximum temperature										
Strategy	2	9.7760	4.8880	1.3711	0.2583	1	0.4891	0.4891	0.2766	0.6014
Year	1	0.4587	0.4587	0.1287	0.7205	1	0.1464	0.1464	0.0828	0.7749
Strategy X Year	3	37.6335	12.5445	3.5187	0.0177	1	0.0066	0.0066	0.0037	0.9517
Error	106	377.8990	3.5651			47	83.1129	1.7684		
Total	113	498.5218	4.4117			50	84.5406	1.6908		
Mean temperature										
Strategy	2	4.5252	2.2626	1.9650	0.1452	1	0.0796	0.0796	0.1246	0.7257
Year	1	0.2567	0.2567	0.2229	0.6378	1	0.0140	0.0140	0.0219	0.8831
Strategy X Year	3	18.7368	6.2456	5.4240	0.0016	1	0.0035	0.0035	0.0055	0.9412
Error	106	122.0556	1.5147			47	30.0171	0.6387		
Total	113	161.0861	1.4255			50	30.2590	0.6052		
Mean temperature, TP										
Strategy	2	6.5117	3.2559	2.2675	0.1086	1	0.5399	0.5399	0.5399	0.4661
Year	1	0.2435	0.2435	0.1696	0.6813	1	0.0024	0.0024	0.0024	0.9612
Strategy X Year	3	22.5360	7.512	5.2316	0.0021	1	0.0450	0.0450	0.0440	0.8347
Error	106	152.2051	1.4359			47	47.9951	1.0212		
Total	113	201.2018	1.7805			50	48.8167	0.9763		
Incubation duration										
Strategy	2	15.0089	7.5045	0.5737	0.5639	2	180.0212	90.0106	9.3184	0.0001
Year	1	0.6756	0.6756	0.0516	0.8203	1	138.4083	138.4083	14.3288	0.0002
Strategy X Year	3	71.9517	23.9839	1.8337	0.1406	4	1619.1295	404.7824	41.9053	<0.0001
Error	365	4774.1536	13.0799			754	7283.226	9.66		
Total	372	5143.1280	13.8256			763	21085.584	27.6351		
Nest depth										
Strategy	2	56.1493	28.0747	2.3455	0.0970	2	361.9882	180.9941	12.0960	<0.0001
Year	1	8.3004	8.3004	0.6935	0.4055	1	116.5286	116.5286	7.7877	0.0054
Strategy X Year	3	14.2746	4.7582	0.3975	0.7549	4	412.5015	103.1254	6.8920	<0.0001
Error	427	5111.0226	11.9696			642	9606.335	14.963		
Total	434	5340.4065	12.3050			651	17210.467	26.4370		

Table 10. Two-way ANOVA Results for Differences in Each of Four Hatchling Condition Variables among Three Nest Protection Strategies (in situ, Translocated on Beach, and Hatchery), among Years, and with Interactions between Strategy and Year at Bahía de Jiquilisco, El Salvador (2011–2013) and Estero Padre Ramos, Nicaragua (2010–2013).

Hatchling condition	Bahia de Jiquilisco					Estero Padre Ramos				
Source	df	SS	MS	F	*P*	df	SS	MS	F	*P*
Hatching success										
Strategy	2	14.6111	7.3055	94.8910	<0.0001	2	42.4392	21.2196	289.0541	<0.0001
Year	1	125.5695	125.5695	1631.012	<0.0001	1	5.7982	5.7982	78.9833	<0.0001
Strategy X Year	3	160.0229	53.3410	692.8414	<0.0001	4	48.5422	12.1356	165.3109	<0.0001
Error	74050	5701.0123	0.077			124271	9122.8028	0.0734		
Total	74057	8212.7924	0.1109			124280	9456.8933	0.0761		
Female hatchlings										
Strategy	2	1.3065	0.6533	13.0560	<0.0001	2	180.3257	90.1629	2480.044	<0.0001
Year	1	0.2078	0.2078	4.1523	0.0416	1	31.5238	31.5238	867.1031	<0.0001
Strategy X Year	3	13.8677	4.6226	92.3850	<0.0001	4	419.5761	104.8940	2885.244	<0.0001
Error	39925	1997.6814	0.0500			76168	2769.1138	0.036		
Total	39932	2050.0611	0.0513			76177	9961.9925	0.1308		
Hatchling length										
Strategy	2	0.6700	0.3350	8.0863	0.0003	2	1.7580	0.879	1.7580	0.1725
Year	1	2.6925	2.6925	64.9922	<0.0001	–	–	–	–	–
Strategy X Year	3	0.6282	0.2094	5.0545	0.0017	3	0.5107	0.1702	5.6849	0.0007
Error	5684	235.4782	0.0414			10523	315.0974	0.0299		
Total	5691	257.7871	0.0453			10531	328.5500	0.3120		
Hatchling mass										
Strategy	–	–	–	–	–	2	31.1283	15.5642	7.6427	0.0005
Year	–	–	–	–	–	–	–	–	–	–
Strategy X Year	1	2.4193	2.4193	1.7388	0.1873	3	34.1366	11.3789	5.5875	0.0008
Error	6420	8932.3961	1.391			10424	21228.225	2.036		
Total	6425	9449.7998	1.4708			10432	22523.999	2.1591		